

**COMPOSITION AND SUCCESSIONS
OF BRYOPHYTES AND LICHENS IN
A COASTAL DUNE AREA IN
SOUTHERN SWEDEN**

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COMPOSITION AND SUCCESSIONS OF BRYOPHYTES AND LICHENS IN A
COASTAL DUNE AREA IN SOUTHERN SWEDEN

- I. Composition and successions of bryophytes and lichens in an outer coastal dune area in southern Sweden.
- II. Composition and successions of lichen communities in an inner coastal dune area in southern Sweden.
- III. Frequency determinations with different quadrat sizes in two plots abundant in lichens in a coastal dune area in southern Sweden.

Magnus Magnusson

COMPOSITION AND SUCCESSIONS OF BRYOPHYTES AND LICHENS IN AN
OUTER COASTAL DUNE AREA IN SOUTHERN SWEDEN

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1 INTRODUCTION

Coastal expanding dune areas offer ideal opportunities for investigations of plant colonizations and successions. A sequence of successively older dune ridges with pioneer vegetation stages at the shore and with increasingly older vegetation landwards make such areas "natural laboratories" for succession studies. Already in the nineteenth century classical investigations of the structure and succession of vegetation on dunes were made by Warming (1891 and later) and by Cowles (1899). In studies on Danish dunes, Warming (1909) demonstrated the importance of cryptogams and distinguished dunes dominated by mosses and lichens as special types ("mosklitter" and "lavklitter" respectively). He established that mosses had an important role as sand-fixers. In later studies bryophytes and lichens have interested workers not only for their usually great abundance but also with regard to relationships between field layer and bottom layer successions. For example, Birse and Gimingham (1955), found that on young dunes the moss colonization was carried out mainly by species with an upright growth habit with ability to endure some sand accretion. On old fixed dunes with an open phanerogamic vegetation, mosses with a mat growth form reached their greatest importance, while in the final stage - the dune pasture with a nearly complete cover of vascular plants - weft mosses dominated. Richards (1929) found interactions not only between the bottom and the field layers but also between the bryophytes and lichens themselves. Mosses were the pioneers and prepared the ground for the lichens through the formation of carpets. The lichens gradually increased in abundance on older dunes while the mosses declined in importance. In the final stage, however, the lichens were superseded by the closed phanerogamic vegetation while the mosses could regain their dominance.

In this investigation the bryophyte and lichen vegetation will be described in a coastal dune area in south Sweden with distinct dune ridges of different age with the following aims:

1. To analyse the distribution of lichens and bryophytes in relation to that of the vascular plants and to the topography.
2. To search for bottom layer successions both those caused by the cryptogams themselves and those caused by interaction from the vascular plants.

2 SITE DESCRIPTION

The study area is located on coastal dunes at Sandhammaren (14°11'E and 55°22'N) in southeastern Skåne, southernmost Sweden. The vegetation of the dune area at Sandhammaren has been described by inter alia Olsson et al. (1971) and Olsson (1974). The area is composed of an outer part with primary dunes, often as ridges parallel to the shore, and an inner part with secondary irregular dunes. On the outer dunes the vegetation cover is continuous and forms a grass zone (Ammophila arenaria and A. baltica) and a dwarf shrub heath (Calluna vulgaris and Empetrum nigrum) with scattered trees (Betula verrucosa, Pinus sylvestris and Quercus robur). On the inner dunes birch fens (in wet depressions) oak woods and pine woods and Calluna-Empetrum heaths are intermingled with patches of sand, either bare or stabilized by Corynephorus canescens. The human influence on the secondary dune landscape was earlier great as a consequence of destruction of original forests and grazing (Olsson 1972).

The site chosen for this study is situated 1.0-1.3 km SSW of the lighthouse at Sandhammaren in an area with dune ridges extended in an approximate west-eastern direction and parallel to the sea (Fig. 1). At the most five distinct ridges can be distinguished (excluding the mobile outermost ridge). Of these number three is the most pronounced and numbers one and four

(counted from the sea shore) are missing in part of the area (Fig. 2). The innermost ridge, bordering on a birch fen, is partially eroded and contains depressions forming a transition to the inner dune landscape. The first ridge was formed during 1962-69 and the second one during 1959-61 (Wallén 1980).

The distinct zonation of the vegetation also implies a succession (Olsson et al. 1971, Olsson 1974) that starts with dune building and sand stabilization by Ammophila arenaria, A. baltica and to a lesser degree by Elymus arenarius. The reduced sand accretion may lead to the appearance of Corynephorus canescens, which is common especially in exposed sites. The next stage is the invasion of Calluna vulgaris and Empetrum nigrum which gradually form a dwarf shrub heath which is later invaded by birch (Betula verrucosa). The final stage is either an oak wood or pine wood that is formed by colonization of the Calluna-Empetrum heath. The pine is not native to the area but spreads from plantations.

A small road crosses the Calluna-Empetrum heath between the two innermost ridges and paths connect this road with the sea. In the eastern part of the area there is a small cottage. Some years ago an area about 100 m in length was accidentally burnt off on the innermost ridge to the west of the cottage.

3 METHODS AND NOMENCLATURE

The vegetation was analysed by means of 0.25 m^2 quadrats along 7 transects at right angles to the ridges. The quadrats were permanently marked and sampled during July - October 1975 with additional studies of the bottom layer during the summer of 1976 after laboratory examinations of collected material. The transects were 200 m in length, apart from one that was 150 m, and were laid out in undisturbed areas. The distance between the transects varied between 30 and 80 m (Fig. 2). All but one of the transects start with the foredunes and end where the birch fen begins. The deviating transect ends near the road thus excluding the innermost ridge. The quadrats were placed at intervals of 5 m along the transects except near paths and near the road where the quadrats were transferred to the nearest unaffected spot. Additional quadrats (9 and 8) were chosen subjectively and analysed in October - November 1976 for the description of two communities for which no and only one sample respectively had been obtained along the transects. These communities, the Cladonia glauca - C. chlorophaea community on dead Calluna and the Dicranum scoparium community, are in mosaics with the dwarf shrubs and a sufficient number of homogeneous samples could only be achieved by increasing the number of transects considerably.

The cover was estimated in percent classes (<1, 1...5, 10, 20...100). Branches of trees on a level higher than one metre were assigned to the tree canopy.

Quadrats representing zones of the transects with corresponding vegetation and exposure were combined and frequency and mean cover (%) were calculated. A classification of the bottom layer was made in the field and the communities were described by homogeneous samples from the transects along with the additional subjectively chosen ones. Frequency and characteristic mean cover (%) (Malmer 1962) were calculated. The neutral term community is used for the distinguished vegetation types in this local investigation.

The transects were leveled in the autumn 1977. An ordination comprising all vegetation of one representative transect (4) was made in order to demonstrate the influence of topography on the sequence of the quadrats from the shore and inland. This was performed by the principal component programme ORDINA (Roskam 1971; see also Persson 1978), which uses a normalized Euclidean distance $\frac{ED}{\sqrt{N}}$ as a dissimilarity index. The original cover data produced a less satisfactory ordination with many coincident quadrats and thus a transformation was made i.e., $100(1+\text{LOG}\%)$ (see Jensen 1978).

The variation in mean number and mean cover of species groups per quadrat and zone is calculated as 95% confidence limits $(\pm t \cdot s)$.
 $\sqrt{N}$

The nomenclature for vascular plants follows Lid (1974) except for the sand-living form of Festuca rubra which is here called F. arenaria. Salix repens var. nitida is here called Salix arenaria and the hybrid between Ammophila arenaria and Calamagrostis epigeios is called Ammophila baltica. The nomenclature for bryophytes follows Arnell (1965) and Nyholm (1954-69) except for Dicranum rugosum, which is called D. undulatum, and for lichens Dahl & Krog (1973). For practical reasons some simplifications were made in the species identification. Cladonia chlorophaea may include C. pyxidata as in a few cases a positive reaction with paraphenylenediamine was registered, Cladonia floerkeana may include C. bacillaris and Cephaloziella divaricata may include also some other Cephaloziella species. Lecanora subfusca coll., which is common on dead Ammophila and Calluna but quantitatively insignificant was disregarded.

4 RESULTS

4.1 Distribution of the species

The outermost dune ridge (zone 1) dominated by Ammophila arenaria and A. baltica with mobile sand has no mosses or lichens (Table 1).

In the next zone, which is dominated by the dune grasses among the vascular plants in addition to Corynephorus canescens, the dunes are stabilized and humus begins to accumulate on the ground. At the same time the first bryophytes and lichens appear. They are relatively frequent but have usually low cover. The bryophytes are inferior to the lichens both in number and quantity. Among the more common species, Pohlia nutans, Cephaloziella divaricata, Dicranum scoparium and Ceratodon purpureus may be mentioned. The lichens utilize the Ammophila litter as a substrate. Hypogymnia physodes colonizes already while the dead leaves of Ammophila are still upright while other species such as Cladonia chlorophaea, C. glauca, C. subulata and C. cornuta colonize the litter on the ground.

The same vascular plants dominate also on the north slope of second ridge (zone 3) with isolated occurrences of Calluna vulgaris and Empetrum nigrum as the most conspicuous new species in the field layer. The dominance of lichens in the bottom layer is here still more pronounced than in the previous zone. Cladonia glauca and C. chlorophaea dominate while C. cornuta, C. subulata, Hypogymnia physodes, C. coccifera, C. floerkeana are frequent species with usually lower cover values. Cephaloziella divaricata, Pohlia nutans and Dicranum scoparium are relatively common while other species, for instance Pleurozium schreberi and Dicranum undulatum are scattered.

Also on the steep south slope and on the summit of the third ridge (zone 4) the dune grasses dominate together with

Corynephorus canescens with Calluna vulgaris and Empetrum nigrum scattered on the summit. This site is unfavourable especially for bryophytes which are reduced both in number and quantity. The lichens may be insignificant or poorly represented by species found in the previous zones. Cornicularia aculeata is rather common on the summit and along windfurrows in the lower part of the slope.

The north slope of the third ridge (zone 5) is mainly occupied by an open Calluna-Empetrum heath with invading trees, mostly birch (Betula verrucosa) but also pine (Pinus sylvestris) and to certain degree oak (Quercus robur). On the upper part of the slope the dune grasses increase in importance. Of the bryophytes, Dicranum scoparium is the most striking. This species forms mats between the dwarf shrubs. Another mode of growth is demonstrated by Pleurozium schreberi which entangles with the dwarf shrubs. Dicranum undulatum is found together with both Dicranum scoparium and Pleurozium schreberi. The most striking feature among the lichens is the increasing abundance of the Cladina group represented by Cladonia impexa. The species grows mostly in associations with Dicranum scoparium but also entangled with the dwarf shrubs and in the upper part of the slope together with representatives of the Cenomyce group already encountered in the outer zones. Hypogymnia physodes is common both on aging Calluna twigs and in association with Dicranum scoparium.

The gentle south slope of ridge four (zone 6) is dominated by a sparse dune grass vegetation together with Carex arenaria and Corynephorus canescens. Calluna vulgaris has invaded the slope in the eastern part of the study area on less sloping ground. Cladonia species of the Cenomyce group dominate the bottom layer. Cladonia impexa forms mats here and there. Among the bryophytes Cephaloziella divaricata is common while Dicranum scoparium is more scattered.

The north slope of ridge four (zone 7) is covered by a closed Calluna-Empetrum heath with vigorously growing dwarf shrubs and with scattered tree saplings. Here, Pleurozium schreberi is the most common bottom layer species, often in mosaics with Cladonia impexa. The small Cladonia species are sparse in this zone. Hypogymnia physodes is common as an epiphyte on Calluna twigs.

The Calluna-Empetrum heath, with scattered tree saplings, occupies the largest part of the area between ridges four and five (zone 8). Small patches are dominated by dune grasses or Corynephorus canescens. Calluna vulgaris is often degenerated and patches with litter from dead heather are in mosaics with fresh material. Such a degeneration is restricted mainly on level ground or ground exposed to the south and is particularly characteristic for this dune heath. The colonization of the litter from dead heather resembles that on litter from the dune grasses. The small Cladonia species dominate together with Hypogymnia physodes, Dicranum scoparium and Cladonia impexa (Table 2). The latter species forms mats which often lose vigour and darken. The cryptogamic vegetation in dense heath is often reduced with scattered occurrences of for instance, Hypogymnia physodes, Cladonia impexa, C. glauca, C. chlorophaea, Dicranum scoparium and Pleurozium schreberi. Patches with well developed mats of Cladonia impexa and Pleurozium schreberi are however frequent as well. On grass-covered patches Cornicularia aculeata, Cladonia mitis, C. impexa, C. glauca and C. chlorophaea are striking.

The border between the heath and the sparse Ammophila and Corynephorus vegetation (zone 9) on the innermost eroded ridge is often indistinct as Calluna vulgaris in many places ascends the slope. Similarities with dunes localized further inland, characterized by depressions and bare sand surface, are also obvious in the lichen flora. Cladonia mitis and C. uncialis, with main distributions in the investigated area on this ridge, are common and are often

accompanied by Cornicularia aculeata and Lecidea uliginosa, these species being characteristic of the dunes further inland (Magnusson 1981). The small Cladonia species are again encountered where grass litter has accumulated and Dicranum scoparium forms mats on north slopes of blowouts.

The north slope of the innermost ridge (zone 10) is covered by a Calluna-Empetrum heath except below trees (primarily birch) where the sparse field-layer reveals mainly Calamagrostis epigeios, Poa pratensis, Melampyrum pratense and Convallaria majalis. Pleurozium schreberi dominates the bottom layer while Cladonia impexa is often scattered in the upper part of the slope. The cryptogamic vegetation in areas shaded by trees is very sparse and consists of a few mosses such as Dicranum scoparium and Aulacomnium androgynum.

4.2 The cryptogamic plant communities

The cryptogamic vegetation has been classified into 4 communities (Table 2).

The Cladonia glauca-C. chlorophaea community has its main distribution on stabilized Ammophila dunes but occurs also on patches with dead Calluna. The environmental requirements are the same in both types of sites - an open habitat with litter-covered ground. On the fixed Ammophila dunes two types can be distinguished. One is distributed in zones 2-4 with its optimal development on the north slope of the second ridge (zone 3). Cladonia glauca and C. chlorophaea codominate while Cladonia cornuta, C. coccifera, C. floerkeana, C. subulata and Hypogymnia physodes appear as regular associates but with lower cover values. Bryophytes, above all Cephaloziella divaricata and Pohlia nutans, are inferior to the lichens and dominate only on small patches. The other type occupies more exposed sites than the former one, nearly exclusively on the south slope of the fourth ridge (zone 6) but also scattered on the south slope of the innermost ridge (zone 9) and on

spots in the heath dominated by dune grass (zone 8). Besides the abundance of Cornicularia aculeata the increasing importance of Cladina species, Cladonia impexa and C. mitis, is striking. On the south slope of the fourth ridge a micro-community can be distinguished where "cushions" of Cephaloziella divaricata are overgrown by Cladonia glauca, C. coccofer, C. cornuta and C. chlorophaea. The Cladonia glauca - C. chlorophaea community on patches with dead heather is dominated by these species together with Hypogymnia physodes. The latter species is already common on upright twigs of degenerating heather. The Cladina group is well represented by Cladonia impexa. Dicranum scoparium is the only bryophyte of importance.

Several of the species included in this community are common and characteristic on acid Ammophila dunes in Western Europe, e.g., Cladonia glauca, C. chlorophaea, C. pityrea, C. scabriuscula and Cephaloziella divaricata. These species are, however, not restricted to dune areas but can be found in other habitats as well.

The Cladonia impexa community has its optimal development in the heath on the north slopes of the three innermost ridges where it is usually accompanied by other Cladina species - in decreasing order of abundance Cladonia tenuis, C. mitis, C. arbuscula and C. rangiferina. A fragmentary type of the community represented by Cladonia impexa alone or together with C. mitis is found in equilibrium with Dicranum scoparium-carpets and on the mixed Ammophila-dunes from the south slope of the fourth ridge and landwards.

The Dicranum scoparium community has its restricted distribution on the north slope of the third ridge where this moss forms mats in the open dwarf shrub heath. Other bryophytes are sparse with Polytrichum juniperinum as the most common associate. The moss carpet is characteristically overgrown by lichens, above all Cladonia impexa, Hypogymnia physodes,

Platismatia glauca, Cornicularia aculeata, Cladonia coccifera and C. chlorophaea.

The Pleurozium schreberi community is best developed on the north slopes of the three innermost ridges as bottom layer in the closed dwarf shrub heath. Pleurozium dominates allowing few other species to be of importance, for instance Dicranum undulatum and Hylocomium splendens on the innermost ridge, and Hypnum ericetorum and Scleropodium purum on the two innermost ridges.

4.3 Species groups

Differentiation within bryophytes and lichens is made according to life strategies. For bryophytes this follows During (1979). The colonists are characterized by, for example, a moderately short life span, a high reproductive effort both as asexual and sexual reproduction and usually a short turf growth form. Included in this group are Pohlia nutans, Dicranum scoparium, Ceratodon purpureus, Aulacomnium androgynum and Cephaloziella divaricata. The latter species, with its strong reliance on asexual reproduction, belongs to a group of species with a strategy that During (op.cit.) considers to be derived from the colonist one but resembles that of shuttle species. Among the characteristics of the perennial stayers are a long life span and a low reproductive effort. This group includes Pleurozium schreberi and its associates (Hylocomium splendens, Hypnum ericetorum, Scleropodium purum, Plagiothecium curvifolium, Brachythecium curtum and Dicranum undulatum).

The two groups of lichens, surface lichens and volume lichens, are distinguished by differences in growth form, rate of spread and competition. The dominating lichens on the outer dunes, i.e., is various members of the Cladonia - Cenomyce group, have in common a rapid spread into a newly formed habitat, a small individual volume and a low competitive ability against other cryptogams and the dwarf shrubs. The group of surface lichens also includes Cornicularia aculeata, Hypogymnia physodes

and Platismatia glauca, species with a thallus more or less pressed to the substrate and therefore susceptible to overgrowing. The volume species, primarily representatives for the Cladonia-Cladina-group, can compete with other cryptogams and are able to form mats in the heath. The two other species included in the volume species group, Cladonia uncialis and Cladonia gracilis, also appear as colonists of bare sand.

4.4 Mean number of species

The mean number of field layer species per 0.25 m^2 and zone fluctuates only slightly after an initial increase in the earliest zones, while the corresponding mean number of the bottom layer species is more variable (Fig. 3a). In the three outermost stabilized zones the mean numbers of lichen and bryophyte species vary in parallel (Fig. 3b) which strengthens the fluctuations for the combined mean number of the bottom layer species. In the inner zones the fluctuations in species numbers of lichens and bryophytes are instead inversed and the total number of bottom layer species remains rather constant, but with a low value in the innermost zone.

The mean number of lichen species per 0.25 m^2 (Fig. 3b) exceeds those of both vascular plants and bryophytes with exception for the north slope of the innermost ridge. Especially high numbers are found on the north slope of the second ridge and on the south slopes of the two innermost ridges. Low numbers, on the other hand, are found in the innermost zone and in the outermost stabilized zone. There are indications of a maximum in the middle of the transect, a finding that is in agreement with results of van der Maarel and Leertouwer (1967) that the highest diversity is reached in the middle of an environmental gradient. The surface lichens make up the bulk of the number of lichen species (Fig. 3c). The variation in number of the surface lichen species resembles that of total lichens, but, with a decreasing trend landwards. The volume lichens (Fig. 3c) already exist in the earliest stabilized zone but are very

scattered. After a steady increase in number landwards a nearly constant value is reached from the south slope of the fourth ridge and to the north slope of the innermost ridge, where the mean again falls. The mosaic of Cladina mats and dominating Pleurozium mats on the innermost north slope causes a large variation in number of volume lichens per quadrat.

The mean number of bryophyte species per 0.25 m^2 (Fig. 3b) is throughout higher on the north slopes than on the south slopes (most pronounced on the third and fourth ridges and to a lesser extent on the innermost ridge). In addition, the mean number is low in the outermost stabilized zone. The mean number is composed to about the same extent of colonists and perennial stayers (Figs. 3d, e). The colonists represent the bryophytes nearly exclusively in the three outermost stabilized zones with a maximum on the north slope of the second ridge. The low mean value on the south slope of the third ridge is also of interest. From the north slope of the third ridge and up to the north slope of the innermost ridge the numbers slowly decrease. Colonists still exist on the innermost ridge although with a low mean number per 0.25 m^2 . The stayers do not appear until the north slope of ridge two and then in very low numbers. They are entirely absent from the south slopes of the third and fourth ridges and are sparse on the south slope of the innermost ridge.

4.5 Mean cover

The mean cover curve of field layer species per 0.25 m^2 and zone (Fig. 4a) shows that the dune grasses on the outer dunes with a seemingly continuous vegetation cover occupies only 10-30% of the ground while the dwarf shrubs contribute to an increasing ground cover with a maximum in the heath between the two innermost ridges where the vegetation cover of the field layer averages 70%. Lower cover values are prevailing in zones with both dune grass vegetation and dwarf shrub heath (zones 5, 6 and 9) and in the innermost zone where parts of the heath are shadowed by an increasing tree layer.

The patchy colonization of the dwarf shrubs is reflected in a large variation between the samples (especially in zones 6 and 9). The mean cover of the bottom layer species (Fig. 4b) may be of the same magnitude as that of the field layer where this is sparse. A maximum is indicated in the middle zones where the dwarf shrub heath is still open (zone 5) and in the Ammophila vegetation on the south slope of ridge four (zone 6). The lichens dominate the bottom layer in dune grass vegetation (zones 2-4, 6 and 9) while the bryophytes co-dominate the bottom layer in dwarf shrub heath (zones 5, 7, 8 and 10) (Fig. 4c and 4d). The surface lichens and colonist bryophytes have their main distribution in the outer and middle zones (Fig. 4e) but with a low mean cover value on the south slope of ridge three. The volume lichens and stayer bryophytes are mainly distributed in the middle and inner zones with pronounced maxima on the north slopes (Fig. 4f).

The variation in mean cover of lichens (Fig. 4c) is less than the variation in mean number. There are two fairly diffuse maxima on the north slope of the second ridge and on the south slope of the fourth ridge. Large variations between the samples indicate distributions in patches on both slopes of the fourth ridge and on the north slope of the innermost ridge. On the other hand, there is only a small variation in the outermost stabilized zone where the quadrats contain almost equally small amounts of widely scattered lichens. The mean cover curve of surface lichens (Fig. 4g) is largely that of lichens. The maximum for surface lichens on the north slope of the second ridge is somewhat more pronounced and there is a decreasing trend landwards. The mean cover of volume lichens (Fig. 4h) is generally low with slightly higher values on the north slopes of the three innermost ridges. In contrast to the surface lichens, the volume lichens have a low mean cover on the south slope of the fourth ridge.

The variation in mean cover of bryophytes (Fig. 4d) resembles that of the mean number. The main difference is the low

contribution of the colonists to the cover in relation to mean species number in the three outer stabilized zones and on the south slopes of the two innermost ridges, where they completely or almost completely so represent the bryophytes. The poor agreement between mean number and mean cover of the colonists is evident by comparing Fig. 3d and 4i. The colonists are widely scattered, usually with a small individual cover except on the north slope of the third ridge where Dicranum scoparium causes a cover maximum. Where the stayers are present they also have a high cover which explain why the mean number curve and mean cover curve are of a similar appearance (Fig. 3e and d, 4j, respectively).

4.6 Topography and vegetation differentiation along transect four

The ordination of the sampling quadrats from transect four (Tab. 3) revealed a so-called bell-shaped curve form (Fig. 5) as discussed in, for instance Swan (1970). The extracted variances for the first four dimensions in the ordination are 28, 19, 9 and 8% respectively, or together 64%, thus 47% of the total variation being presented through the two first axes. The sampling quadrats are arranged from the foredunes at one end, followed by successively older stages through to the lower part of the north slope of the innermost ridge at the other end. However, due to the topography the sequence of the sampling quadrats is changed in some cases. The retarded vegetation development on the south slopes has the result that sampling quadrats at this position along the transect (12-13, 19-21, 25, 33-34) are placed near quadrats representing earlier stages. In the outer zones the wind contributes to keep the vegetation in a colonizing stage with Corynephorus canescens dominating and a scattered bottom layer through forming furrows that are especially common along south slopes (quadrats 12 and 13). On the innermost ridge an eroded and bare sand surface with vegetation in a recolonizing stage (quadrats 33 and 34) probably is a result of earlier human activities. In contrast an accelerated

development can be observed on the south slope of the third ridge where vegetation can be found resembling that further inland (quadrat 24).

5 DISCUSSION

5.1 Abundance relations

The obvious maximum in mean number of lichen species per quadrat on the south slope of ridge four is the result of a high cover but also of a high number of available species, several with high frequencies (Table 1). The position of the slope along the transect implies possibilities both for the establishment of surface lichens and volume lichens. The colonization proceeds largely over an area with only small interactions from the scattered dwarf shrubs and bryophytes.

The bryophytes are certainly represented both by colonists and perennial stayers on the north slope of ridge three (zone 5) where they have a cover maximum, but this is largely caused only by one species (Dicranum scoparium). The other species are more scattered (often restricted to the dwarf shrubs), which is why a high number of species per quadrat cannot be reached.

An expected increase in number of vascular plants per quadrat where the dune grass vegetation and dwarf shrub heath are intermingled does not occur due to the dominance of one or other of the vegetation types being too great in the meeting zone. The dominance of the dune grasses on the north slope of ridge two and the dominance of the dwarf shrub heath on the north slope of ridge three are probably due to a wide gap in time between these ridges.

The low competitive ability of the surface lichens against the vascular plants is most evident when comparing the

greatly inversed variation inland in mean species number of the former with the variation in mean cover of the latter. The small variation in the mean number and mean cover of the volume lichens indicates a more independent relation between this group and the vascular plants. The dry conditions on the south slope of the fourth ridge may be responsible for a low cover here. According to Ahti (1961) Cladonia impexa, the dominating volume lichen here, is dependent upon a constant humidity of the air. The lower mean number of volume lichens is primarily caused by a lower available number of species and to a lesser degree by a larger individual size.

To judge by the slow decrease in the mean number of colonist bryophytes inland the influence of the vascular plants on these cryptogams would be small. The mean cover, however, reveals that the colonists attain a peak cover value at a certain stage where the considerable increase in ground cover of the vascular plants is initiated by the invasion of the dwarf shrubs. The variation in mean cover and mean number of the perennial stayers illustrate the dependance of these bryophytes on the moist conditions that are achieved as a result of topography (north slopes) and a dense field layer vegetation.

The abundance and distribution on Ammophila dunes among the cryptogamic groups seem to be primarily determined by environmental conditions and less by direct competition between the small species. That the lichens can dominate over the bryophytes on Ammophila dunes is surely a result of a better drought resistance in an environment exposed to extreme drying, at least on south slopes.

In dwarf shrub heath with a less extreme environment for the bottom layer the relative amounts are regulated by direct competition between the larger species present here with a continuous growth in such a way what the bryophytes are superior on the moister sites, with the result that lichens must put up

with the drier sites. As a result of the dry conditions caused by the sandy material, lichens can codominate with the bryophytes on the northern slopes. Investigations on eskers (Påhlsson 1969, 1971) with mixed soil fractions have shown that lichens are abundant on south slopes but are only scattered on north slopes where bryophytes are vigorously growing.

5.2 Succession of species

The simultaneous colonization on the outermost stabilized dunes at Sandhammaren of lichens and bryophytes differs from the conditions along Western European dunes where a pioneer moss stage with for instance, Tortula ruralis, generally is found (Böcher 1969, Chapman 1964, Ellenberg 1978). The early mosses both consolidate the sand surface and leave organic material (Ducker 1960, Ellenberg opcit.) thus preparing the ground for the lichens. While Richards (1929) found young lichen thalli nearly always in moss tufts and therefore regarded the pioneer mosses as necessary for the lichen colonization, Alvin (1960) also found colonizing lichens associated with grass debris. The importance of humus (e.g., from Ammophila and mosses) for the establishment of lichens was further emphasized by Brown & Brown (1968, 1969) when they found that an increasing stability and humus content of the sand was related to increasing cover and species diversity. At Sandhammaren the roles of the pioneer mosses are wholly taken over by the dune grasses.

Alvin (1960) remarked that the more important Cladonia species on the young dunes produced soredia and regarded this feature as a way of achieving rapid establishment in an environment exposed to inundation by sand. Also at Sandhammaren the lichens on the outer dunes are sorediate, a feature that ought to be regarded as an advantage for a rapid and extensive colonization as sand accretion is of minor importance inside the mobile ridge. By means of an abundant

production of many small propagules which contain both the alga component and the fungus component, the sorediate species arrive before more competitive but more slowly colonizing cryptogams and vascular plants. A colonization over a large area may be an advantage in an unpredictable environment such as this, which is exposed to wind and water. The main reason for the low occurrence of the Cladina species on the outer dunes is probably a less effective mode of propagation. The generally more exposed conditions on the outer dunes may contribute to a low abundance of the dominating species Cladonia impexa on account of its dependence on a constant humidity (Ahti 1961). More protected and moister conditions are, however, certainly present on the north slope of the second ridge. Cladina species propagate through thallus fragmentation, conidia and ascospores (Ahti 1961) of which the spores need association with an alga for establishment. These species form a large biomass and a late colonization, when the conditions are more stable is probably an advantage.

In the bryophyte colonization process a combination of differences in mode of propagation and in moisture requirements seems to be of importance. While the pioneer bryophytes (colonists) regularly form propagules, spores or gemmae, species included in the perennial stayers only rarely form sporophytes. Although two species belonging to the latter group, Pleurozium schreberi and Dicranum undulatum, have been noted together with the dune grasses, the perennial stayers are otherwise so intimately associated with the dwarf shrub heath, that an expansion outside this habitat appears unlikely. Through an increased water-holding capacity due to accumulation of humus and increasing wind protection a more stable microclimate can be expected in the heath than in the grass vegetation. Less varying moisture conditions probably also explain why Dicranum scoparium forms carpets in the open north-facing dwarf shrub heath and is only scattered on the outer dunes. In addition, a necessary condition is that this moss can colonize and expand before the more competitive Cladina species (mainly Cladonia impexa). Gimingham & Robertson

(1950) include the growth form of Dicranum scoparium in the tall turfs, which is important especially where the humidity is high. Thus a moisture gradient in addition to a sand accretion gradient was suggested by Birse & Gimingham (1955) to explain the main trends in the distribution of three bryophytic stages on dunes with the dominating growth forms: Short turfs (most important species Bryum pendulum), mats (most numerous species Brachythecium rutabulum) and wefts (for instance Hylocomium splendens and Pleurozium schreberi).

It is interesting to note that in the innermost zone, where the invasion of birch means a further step in the succession of the vascular plants that among the bryophytes thus implies a reestablishment of a colonist stage with, for instance, Dicranum scoparium and Aulacomnium androgynum. The shading from the trees results in a dying off among the heath plants, resulting in open patches which allow some recolonisation of the pioneer bryophytes.

5.3 Succession of communities

The suggested successions are summarized in Fig. 6.

The Cladonia glauca - C. chlorophaea community recognized on Ammophila litter can probably persist for long periods only on south slopes where the invasion of the Calluna-Empetrum heath is strongly retarded. Nevertheless, the community does not escape overgrowing by Cladonia impexa and a slow succession to the Cladonia impexa community may be expected. On north slopes, the competition from the dwarf shrubs and Dicranum scoparium reduces its distribution to the upper dry part of the slope, as can be seen today on ridge three. The Cladonia impexa community is here superior not only to the Cladonia glauca-C. chlorophaea community but also to the Dicranum scoparium community. Through the increasing closure of the dwarf heath the latter communities gradually disappear while patches with Cladonia impexa partly seem to

emerge directly into the heath. On the north slope the increasing closure of the heath foremost implies increasing possibilities for the Pleurozium schreberi community to expand and become dominant in the bottom layer. On level ground the original Cladonia glauca - C. chlorophaea community gradually becomes overshadowed by the dwarf shrubs and a heath originates, either with a very sparse bottom layer, or with Cladonia impexa mats or less commonly with Pleurozium schreberi-mats.

The heath that includes the Pleurozium schreberi community represents a moist growing habitat that is mainly stable. When the heath type with the Cladonia impexa community occupies similar moist habitats it can also be regarded as stable, but when it occupies dry sites such as the type with a sparse bottomlayer it runs the risk of degeneration. The Cladonia glauca - C. chlorophaea community that colonizes patches that originate through such a degeneration is followed by the Cladonia impexa community - a development that closely resembles one described by Böcher (1941, 1952).

The birch intermediate forest type brings about a nearly complete extinction of the heath and its bottom layer as observed today on the innermost ridge. If this stage is followed by an oak wood, a continued sparse cryptogamic vegetation can be expected but if pine forms the final forest stage the light conditions sometimes will be favourable enough to allow Cladonia mats and Pleurozium schreberi mats to develop. These two forest types at Sandhammaren are treated in detail by Olsson (1971, 1974).

6 SUMMARY

The investigation was made in an expanding coastal dune area with successively older ridges extended in a west-east direction. The sand is being stabilized by dune grass vegetation (Ammophila spp.) which part is being replaced in its inner part by a dwarf shrub heath (Calluna vulgaris and Empetrum nigrum) with invading trees (Betula verrucosa, Pinus sylvestris and Quercus robur). Bryophytes and lichens colonize simultaneously. The latter dominate on the outer dunes and are mainly represented by Cladina-Cenomyce group (Cladonia glauca, C. cornuta, C. chlorophaea, etc.). Here the bryophytes are for instance, Pohlia nutans, Dicranum scoparium and Cephaloziella divaricata. On the north slope of the ridge still with open heath, carpets of Dicranum scoparium, and to a lesser degree, of Cladonia impexa cover the ground between the dwarf shrubs. The pioneers still may be found but in the closed heath other species dominate the bottom layer here such as Pleurozium schreberi, Hylocomium splendens, Scleropodium purum, Dicranum undulatum, Cladonia impexa and Cladonia tenuis. On the south slopes with a highly retarded heath colonization, the dune grass vegetation persists with about the same bottom layer as on the outer dunes which, however, gradually becomes overgrown by Cladonia impexa. The final stage in the present-day succession in the area includes oak woods or pine woods.

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TABLE 1. Frequency and mean percentage cover (the exponent) for the species in the different zones. Missing exponent = <1%.

Zone no.	1	2	3	4	5	6	7	8	9	10
<i>Salsola kali</i>	2	.	.	.	.	.	.	.	.	.
<i>Elytrigia juncea</i>	13	2	.	.	.	.	.	.	.	.
<i>Lathyrus maritimus</i>	4	12	3	.	.	.	.	.	.	.
<i>Elymus arenarius</i>	43 ²	29	3	.	.	.	.	.	.	.
<i>Honkenya peploides</i>	4	.	.	.	5	.	.	.	.	.
<i>Festuca arenaria</i>	17 ²	22	31	5	.	.	.	.	.	.
<i>Ammophila baltica</i>	91 ¹⁰	94 ⁵	86 ⁶	80 ²	42	58	.	2	36	.
" <i>arenaria</i>	66 ⁷	94 ⁵	97 ⁵	95 ⁴	32	75 ¹	21	29	50 ¹	.
<i>Hieracium umbellatum</i>	2	39	90	35	32	25	7	14	7	.
<i>Corynephorus canescens</i>	.	55 ⁴	59 ⁴	55 ³	11 ¹	83 ³	7	7	79 ²	.
<i>Jasione montana</i>	.	31	41	5	11	17	.	.	.	.
<i>Carex arenaria</i>	.	2	17	70	84	100 ³	79 ¹	69 ²	71	67
<i>Viola tricolor</i>	.	.	3	.	.	.	.	.	.	.
<i>Helichrysum arenarium</i>	.	.	3	.	.	.	.	.	.	.
<i>Deschampsia flexuosa</i>	.	.	3	.	.	.	.	.	.	.
<i>Empetrum nigrum</i>	.	.	17 ²	10 ³	53 ⁶	.	64 ¹⁹	46 ⁹	7	93 ²¹
<i>Polypodium vulgare</i>	.	.	17	.	58 ¹	8	29	18	.	20
<i>Koeleria glauca</i>	.	.	3	.	5	33	.	.	7	.
<i>Calluna vulgaris</i>	.	.	3	.	74 ³⁰	42 ¹⁶	100 ³⁹	96 ⁵⁴	36 ²²	80 ²⁹
<i>Salix arenaria</i>	.	.	.	.	11 ¹	.	21 ¹	.	14 ¹	13
<i>Lycopodium clavatum</i>	.	.	.	.	5	.	7	.	.	.
<i>Galium verum</i>	.	.	.	.	16	.	.	11	7	.
<i>Betula verrucosa</i>	.	.	.	.	.	.	7 ³	7	.	20 ⁷
<i>Aira praecox</i>	.	.	.	.	.	.	.	4	7	.
<i>Quercus robur</i>	.	.	.	.	.	.	.	7 ⁴	.	13 ⁷
<i>Melampyrum pratense</i>	.	.	.	.	.	.	.	14	.	33
<i>Calamagrostis epigeios</i>	.	.	.	.	.	.	.	4	.	40 ³
<i>Poa pratensis</i>	.	.	.	.	.	.	.	.	.	7
<i>Convallaria majalis</i>	.	.	.	.	.	.	.	.	.	7
<i>Pohlia nutans</i>	.	40	41 ¹	5	21	.	36	.	14	.
<i>Cephaloxiella divaricata</i>	.	30	76 ²	55	37	92 ³	36	36	57	.
<i>Dicranum scoparium</i>	.	16	55	20	89 ¹³	58	86 ²	71 ¹	43	20
<i>Ceratodon purpureus</i>	.	6	3	.	.	.	.	4	.	.
<i>Aulacomnium androgynum</i>	.	2	10	.	16	8	.	.	7	13
<i>Lophocolea heterophylla</i>	.	.	10	.	5	.	7	4	.	.
<i>Polytrichum piliferum</i>	.	.	3	.	.	.	.	4	.	.
<i>Dicranum undulatum</i>	.	.	7	.	63 ²	.	36	11	7	.
<i>Pleurozium schreberi</i>	.	.	7	.	37 ⁷	.	50 ⁸	54 ²	14	80 ¹⁴
<i>Polytrichum juniperinum</i>	.	.	.	.	16	.	.	.	.	.
<i>Plagiothecium curvifolium</i>	.	.	.	.	5	.	7	.	.	7
<i>Hypnum ericetorum</i>	.	.	.	.	.	.	14	14	.	27 ¹
<i>Hylacomium splendens</i>	.	.	.	.	.	.	7	.	.	27 ¹
<i>Brachythecium curtum</i>	.	.	.	.	.	.	.	11	.	7
<i>Scleropodium purum</i>	.	.	.	.	.	.	.	.	.	27
<i>Cladonia chlorophaea</i>	.	81 ²	100 ⁵	90 ³	84 ¹	100 ⁴	86	71	86	27
<i>Hypogymnia physodes</i>	.	88	97	75	100 ²	67	93 ⁶	93 ²	57 ¹	60
<i>Cladonia subulata</i>	.	78	83 ¹	35	5	42	7	11	14	.
" <i>glauca</i>	.	45	83 ⁷	55 ³	53 ³	83 ¹⁵	14	39	43	7
" <i>cornuta</i>	.	55	90 ²	70	84 ¹	92 ²	21	14	36	.
" <i>fimbriata</i>	.	18	7	.	.	.	.	.	.	.
" <i>scabriuscula</i>	.	22	48	10	32	25	21	14	.	.
" <i>coccifera</i>	.	43	66	65	32	92 ²	36	14	71	.
" <i>floerkeana</i>	.	22	62	70	21	75	14	7	21	.
" <i>pityrea</i>	.	18	31	15	21	25	29	11	21	.
" <i>squamosa</i> /glauca	.	10	3	10 ²	26	33	7	14	7	.
" <i>squamosa</i>	.	8	3	10	42	50	50	18	.	7
" <i>impexa</i>	.	4	17	25	63 ³	83 ¹	71 ⁵	71 ³	50 ²	13 ⁵
<i>Cornicularia aculeata</i>	.	.	14	20 ²	11	67	14	7	79 ¹	.
<i>Platismatia glauca</i>	.	.	7	5	16	.	.	.	7	7
<i>Cladonia mitis</i>	.	.	3	.	5	42	7	14	86 ¹	.
" <i>gracilis</i>	.	.	.	.	11	8	7	18	.	7
" <i>arbuscula</i>	.	.	.	.	.	8	.	4	.	7
" <i>tenuis</i>	.	.	.	.	.	.	14 ²	29	7	7
" <i>rangiferina</i>	.	.	.	.	.	.	21	.	.	7
" <i>uncialis</i>	.	.	.	.	.	.	7	.	29	7
<i>Hypogymnia tubulosa</i>	.	.	.	.	.	.	.	4	.	.
<i>Cladonia indet.</i>	.	43	28	40	21	58 ³	36	14	57 ³	.
Bare sand	100 ⁹³	58 ¹²	59 ¹⁴	80 ³⁰	26 ⁶	75 ¹²	7 ⁴	11 ¹	86 ³⁸	0
Cover of canopy layer	.	.	.	.	.	.	.	.	.	20 ¹⁵
No. of samples	47	49	29	20	19	12	14	28	14	15

Height above
mean water level (m)

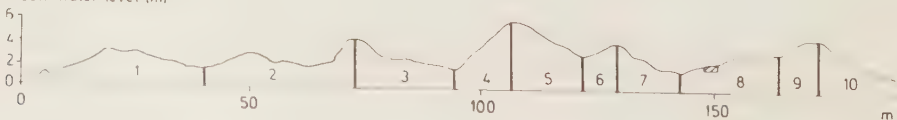


Table 2. Communities. The figures indicate frequency and characteristic mean cover (%) (the exponent). Missing exponent = <1%.

	The Cladonia glauca - C. chlorophaea community		The Cladonia impexa community	The Dicranum scoparium community	The Pleurozium schreberi community
	In Ammophila-vegetation	On dead Calluna			
Ammophila arenaria	91 ⁵	11 ¹	33	44 ²	10
" baltica	86 ²	.	22 ²	.	10
Betula verrocosa	.	.	.	.	20 ³⁰
Calamagrostis epigeios	.	11	11	.	10 ¹
Calluna vulgaris	9	67 ²	100 ²⁸	56 ¹⁹	100 ²⁴
Carex arenaria	36 ²	56 ²	89 ³	56 ²	70
Convallaria majalis	.	.	.	.	10
Corynephorus canescens	73 ⁴	.	.	22 ²	.
Empetrum nigrum	14 ²	22	56 ⁴²	22 ²³	100 ²³
Festuca arenaria	36 ¹	.	.	.	.
Galium verum	.	.	.	.	10
Hieracium umbellatum	77 ¹	.	.	.	.
Jasione montana	41	.	.	.	.
Koeleria glauca	9	.	.	.	.
Lycopodium clavatum	.	.	11 ⁴	.	10
Melampyrum pratense	.	.	.	.	10
Polypodium vulgare	5	22 ⁷	33 ²	.	50 ³
Quercus robur	.	.	.	.	20 ⁵⁰
Salix arenaria	.	.	.	.	30 ⁵
Aulacomnium androgynum	.	.	.	.	10
Brachythecium curtum	.	.	.	.	10
Cephaloziella divaricata	82 ⁴	33	11	22	10
Dicranum scoparium	45	89 ³	67	100 ⁵⁷	40
" undulatum	.	11	11 ²	11 ⁵	30 ²
Hylocomium splendens	.	.	11	.	20 ⁶
Hypnum ericetorum	.	.	11	.	20 ³
Plagiothecium curvifolium	.	.	.	.	10
Pleurozium schreberi	.	22 ⁵	44 ²	11 ¹	100 ⁴⁵
Pohlia nutans	32 ⁴	.	.	.	.
Polytrichum juniperinum	.	.	.	44 ²	10 ¹
" piliferum	5	.	.	.	.
Scleropodium purum	.	.	.	.	30 ¹
Cladonia arbuscula	.	.	22	.	.
" chlorophaea	100 ⁷	100 ¹⁶	78	78	20
" coccifera	91 ²	56 ¹	11	78 ¹	.
" cornuta	100 ²	78	22	67	10
" fimbriata	5	.	.	.	.
" floerkeana	100	78	.	.	.
" glauca	100 ¹²	100 ²⁰	11	33	.
" gracilis	5	.	22	11	10
" impexa	50 ²	89 ⁴	100 ²³	100 ¹⁴	10
" mitis	18 ¹	.	22	22	.
" pityrea	41	11	11	.	.
" rangiferina	.	.	11	.	.
" scabriuscula	45 ¹	.	.	11	20
" squamosa	14 ¹	56	33	22 ²	.
" squamosa/glauca	18 ¹	.	11 ²	22 ²	20
" subulata	91 ²	.	11	.	.
" tenuis	.	.	44 ⁵	.	.
" uncialis	.	.	11	.	.
" indet.	27 ⁴	4 ⁴	11	44 ¹	.
Cornicularia aculeata	41	44	11	67 ²	.
Hypogymnia physodes	86	100 ¹⁰	100 ⁶	100 ⁸	80 ²
" tubulosa	.	11	.	.	.
Lecidea sp.	.	22 ²	.	.	.
Parmeleopsis ambigua	.	11	.	.	.
Platismatia glauca	5	22	11	89 ³	.
No of samples	22	9	9	9	10

The samples representing the Cladonia glauca - C. chlorophaea community in Ammophila-vegetation are from the north slope of ridge 2 and from the south slope of ridge 4, while those on dead Calluna are from the south and north slopes of ridge 4 and from the dune heath between ridges 4 and 5. The samples representing the Cladonia impexa community are from the north slopes of ridge 4 and 5 and from the dune heath between these ridges. The samples representing the Dicranum scoparium community are from the north slope of ridge 3. The samples representing the Pleurozium schreberi community are from the north slopes of ridges 3, 4 and 5 and from the heath between ridges 4 and 5.

Fig. 1. A part of the dune area at Sandhammaren with the investigated area indicated. Note the difference between the outer regular dunes, arranged in ridges, and the inner irregular dunes. The interval between the contours is 2m.



Fig. 2. The transects with the samples indicated (partly missing in zone 1). The zonation is in accordance with Table 1.

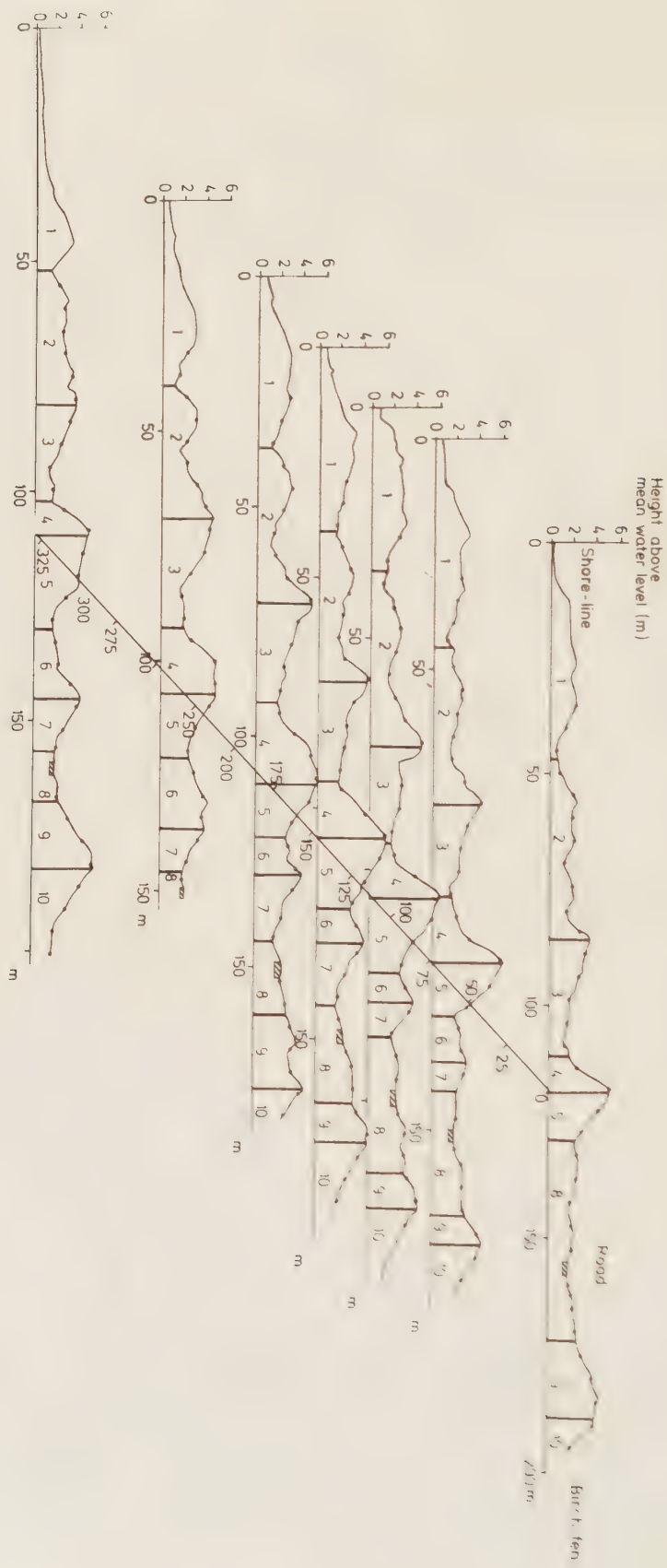


Fig. 3. Mean number of species per quadrat and zone. The vertical bars indicate in both Fig. 3 and Fig. 4 the variation calculated as 95% confidence limits ($\pm t \cdot \frac{s}{\sqrt{n}}$). The number of samples is according to Table 1.

Mean number of species per quadrat

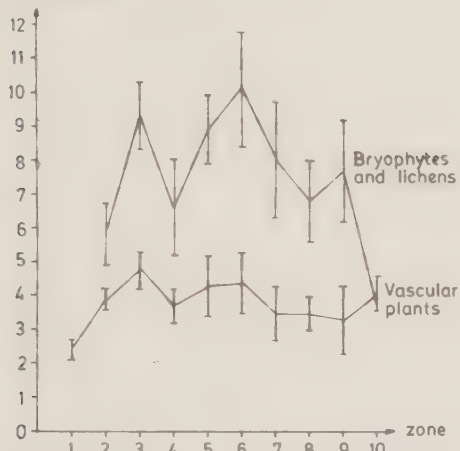


Fig. 3a

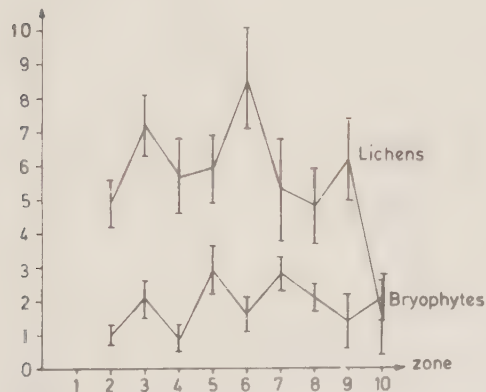


Fig. 3b

Mean number of species per quadrat

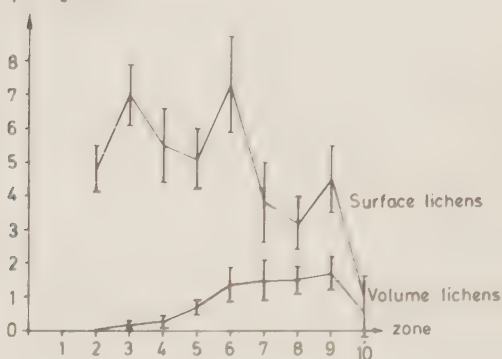


Fig. 3c

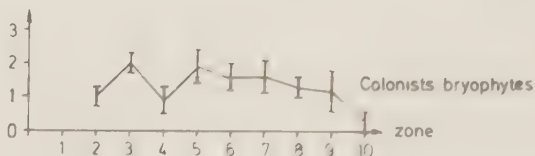


Fig. 3d

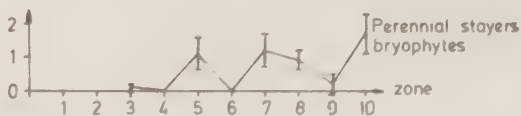


Fig. 3e

Fig. 4. Mean cover of species groups per quadrat and zone.

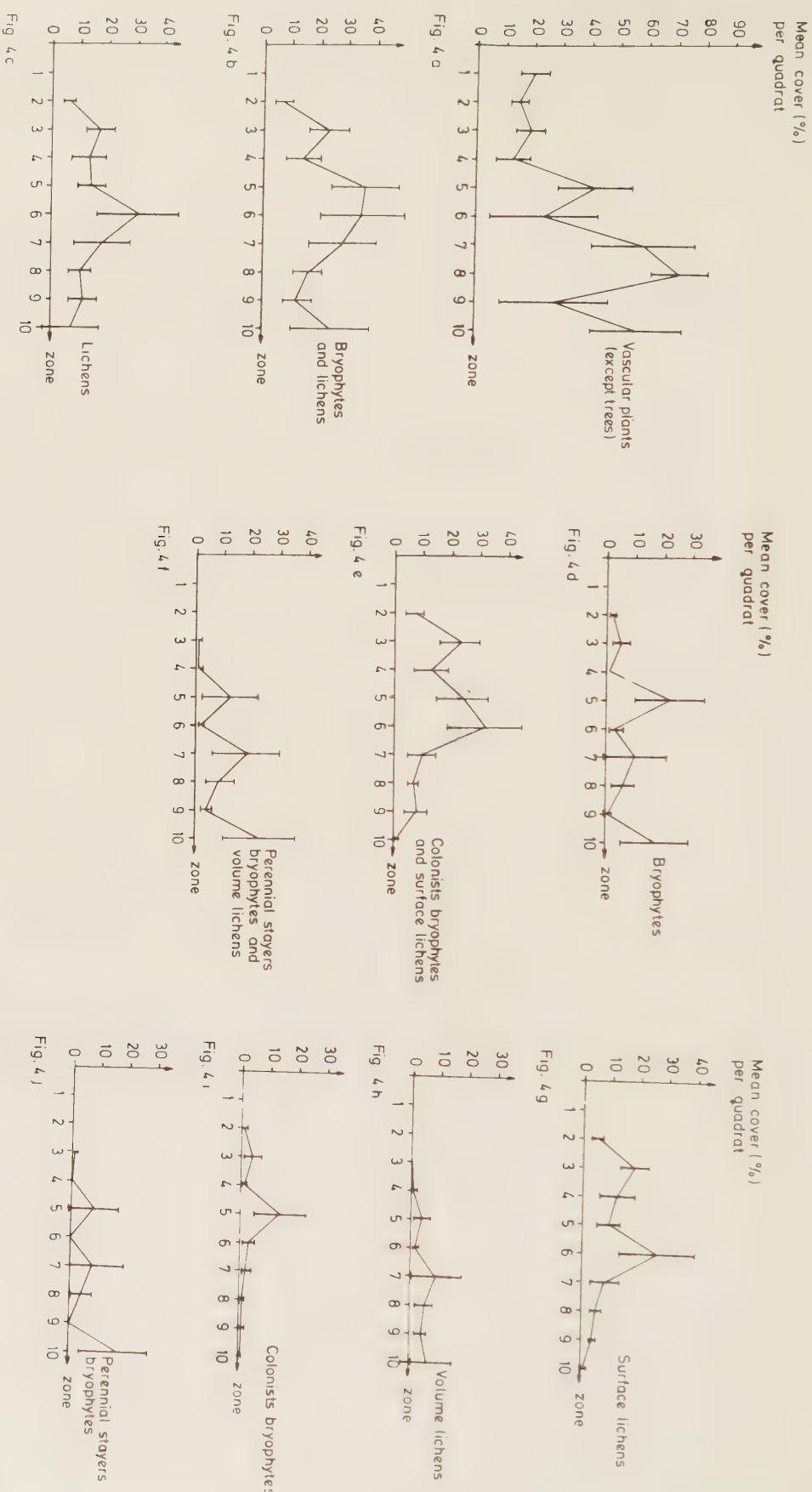


Fig. 5. Ordination of the quadrats along transect four. Filled symbols indicate quadrats that are kept at an earlier stage than the surrounding vegetation on account of topography (south slopes).

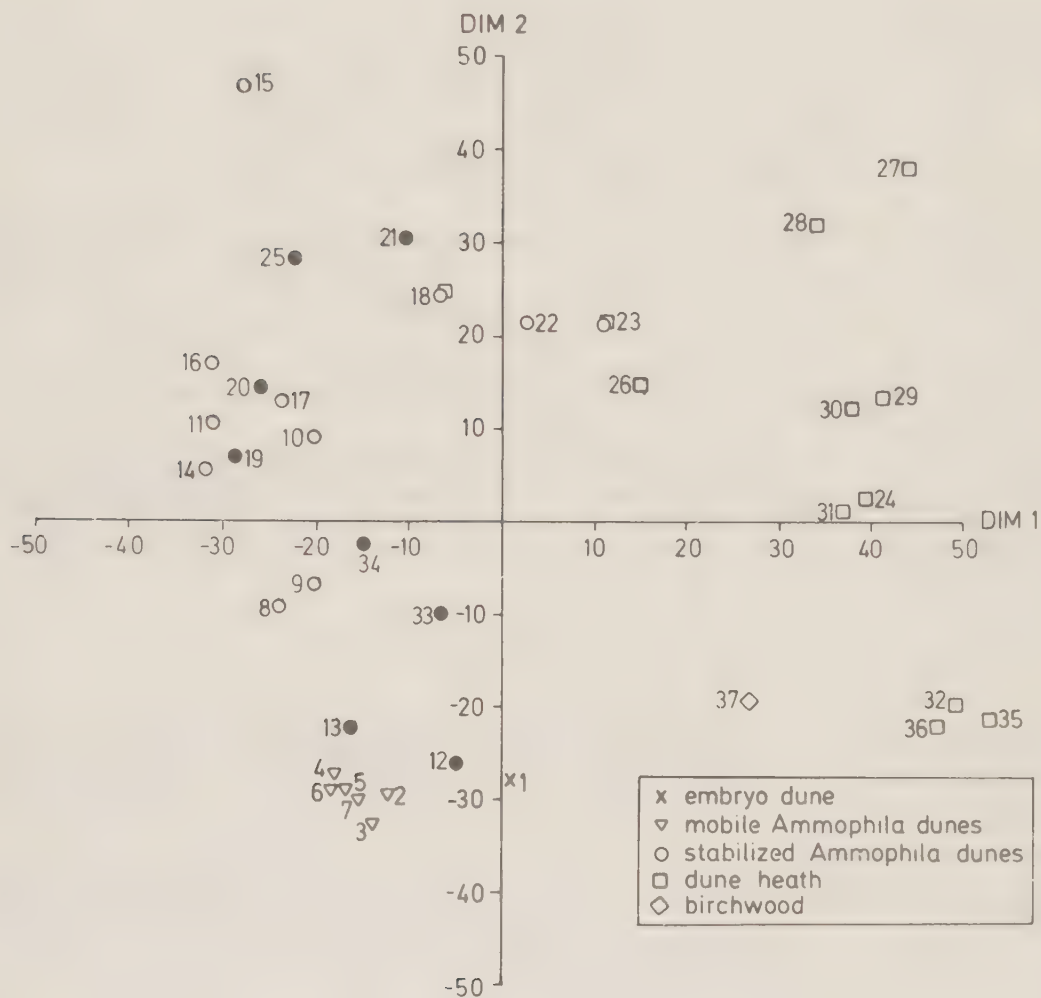
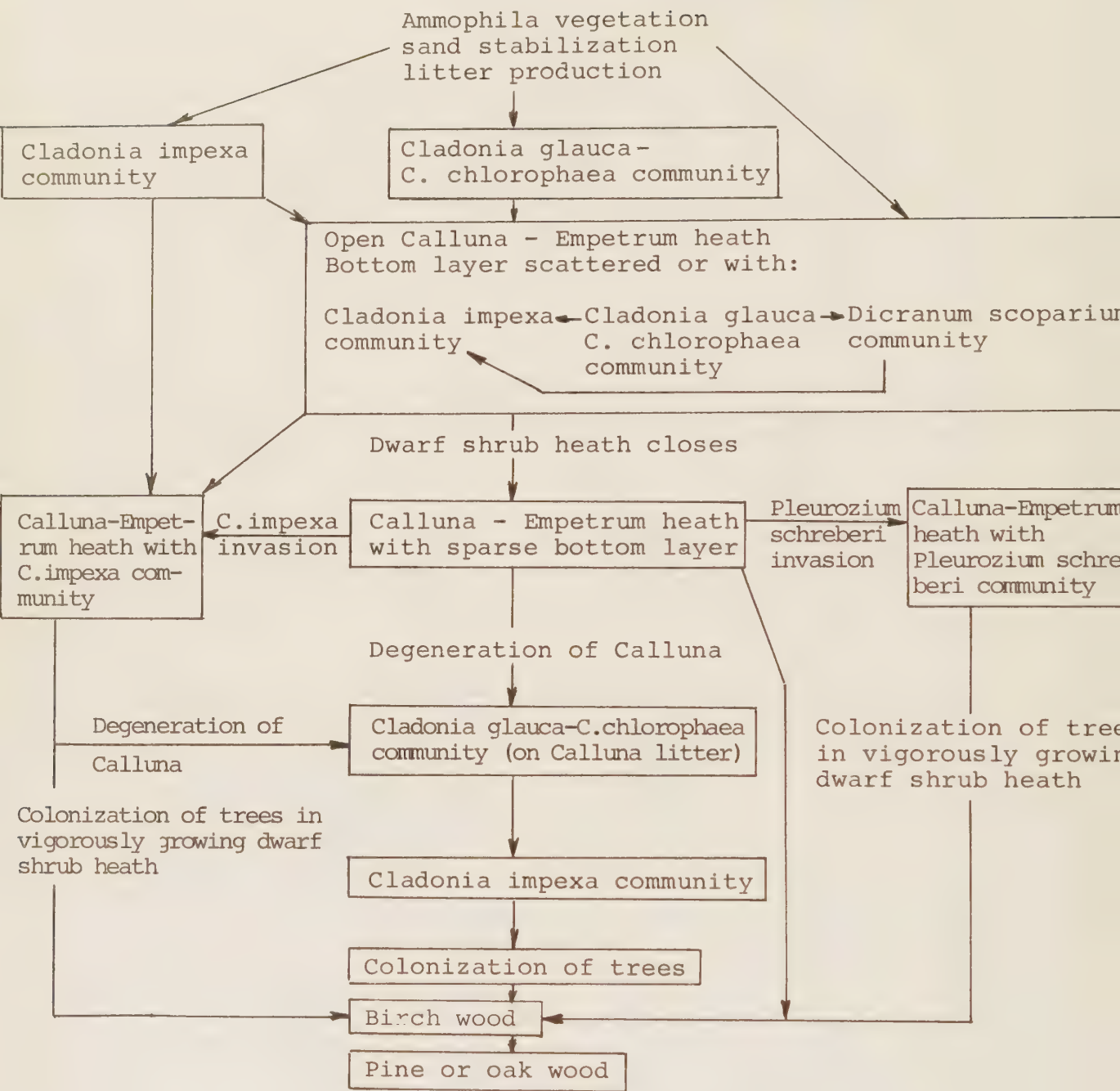


Fig. 6. Suggested successions



COMPOSITION AND SUCCESSIONS OF LICHEN COMMUNITIES IN AN
INNER COASTAL DUNE AREA IN SOUTHERN SWEDEN

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1 Table

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1 INTRODUCTION

Succession and floristic composition of the bottom layer in the lichen-rich Corynephorus canescens community, that colonizes sand, is treated by several authors e.g. Kolumbe 1925, Erichsen 1928, Tüxen 1928 and 1958, Behmann 1930, Krieger 1937, Langerfeld 1939 (investigations from Germany), Böcher 1941 (Denmark) and Stoutjesdik 1959 (the Netherlands). The lichens are usually preceded by mats of Polytrichum piliferum that colonize at the same time or earlier than Corynephorus canescens and Carex arenaria. Also Racomitrium canescens may be the pioneer moss. Sometimes lichens, for instance Lecidea granulosa and L. uliginosa, Pycnothelia papillaria, Cladonia verticillata var. cervicornis and Stereocaulon condensatum and algae may occur as pioneers but they are usually of local importance only. The colonizers are followed either by Cornicularia aculeata or by different Cladonia species. The succession leads in both cases towards lichen mats dominated by some competitive Cladonia species of which C. mitis, C. zopfii and C. impexa are important. Then the bottom layer succession has reached its final stage in the Corynephorus community. However, the succession continues through a slow invasion by Calluna vulgaris and Empetrum nigrum or by seedlings of Pinus sylvestris.

Olsson (1974) has studied the species composition, sociology and vascular plant succession in the Corynephorus community on sand areas in southern Sweden. He regards this vegetation type as an association called Cladonio (destrictae) - Corynephoretum. This association colonizes acid, eroded and aeolian sand and is distributed in Middle and Western Europe with an optimum in northern Germany. Two sub-associations are distinguished (Olsson op.cit.); one where Corynephorus canescens is totally dominating and a bottom layer is absent and the second

(Cladonia subass.) where lichens, especially Cladonia spp. and Cornicularia aculeata, are common.

In an earlier paper the composition and succession of the bottom layer on the outer dunes in a coastal dune area in southern Sweden was described and related to the occurrence of vascular plants (Magnusson 1981). In this study the bottom layer on the inner dunes will be analysed from a successional point of view and Olsson's (op.cit.) structuring will be further developed in a dune area with a well-developed Corynephorus vegetation abundant in lichens.

2 SITE DESCRIPTION

The investigated dune area is situated at Sandhammaren in southernmost Sweden (14°11'E and 55°22'N).

On the outer expanding dunes, which often are arranged in parallel ridges, the sand surface is being stabilized by an Ammophila vegetation. Further inland it is being replaced by a Calluna-Empetrum heath with invading trees (Betula verrucosa, Pinus sylvestris and Quercus robur). This zonation of the vegetation also implies a succession (Olsson et al. 1971, Olsson 1974). The colonization of a bottom layer by bryophytes and lichens, described by Magnusson (1981), proceeds simultaneously. The lichens dominate, forming a Cladonia glauca-C. chlorophaea community, which is associated with debris from Ammophila. The further vegetational succession from this community is indicated by the appearance of Dicranum scoparium and Cladonia impexa as well as by invasion of the dwarf shrubs. On south slopes the heath expands very slowly and here the Cladonia glauca-C. chlorophaea community is preserved although partly overgrown by Cladonia impexa. On north slopes the heath colonization is rapid and a bottom layer develops with either a very sparse cryptogamic vegetation or with carpets of Pleurozium schreberi and Cladonia impexa. The final stage is

regarded to be either an oak wood with scattered bryophytes and lichens or a pine wood, sometimes with well-developed carpets of Cladina species, mainly Cladonia impexa and of Pleurozium schreberi. (Pine was introduced in the area for forestry purpose and nowadays is spreading).

The inner dunes were earlier influenced by human activity through grazing and devastation of trees, thus destroying the vegetation and exposing the sand (Olsson op.cit).

The vegetation today consists of a mixture of Corynephorus canescens patches, birch fens in wet blowouts, oak woods, pine woods and Calluna-Empetrum heaths. The vascular plant succession on such secondary dunes, described by Olsson (op.cit.), usually starts with colonization of the bare sand by Corynephorus canescens and proceeds via a Calluna dominated dwarf shrub heath to either an oak wood or a pine wood. A pine wood may also arise through colonization in the Corynephorus stage.

3 METHODS AND NOMENCLATURE

Twenty homogeneous stands of lichen mats were analysed during June-August 1978 from various parts of the inner dune landscape; with the most distant stands about 3 km apart. The stands were as large as possible to avoid more accidental species combinations and were selected so that most of the variation in floristic composition between different lichen mats would be covered. Within each stand the vegetation was analysed by means of randomly distributed quadrats (size $1/16 \text{ m}^2$) and with the cover for each species estimated according to the Hult-Sernander-DuRietz's scale (DuRietz 1921). The number of quadrats was considered sufficient when the running mean of the mean degree of cover of the dominant species in at least three succeeding quadrats was constant. This was achieved after an analysis of 5-20% of the total stand area. The mean degree of cover was calculated after transforming

the cover values to the middles of the cover classes (1, 3, 6, 12 and 24/32 respectively) and division with all quadrats in the stand. The value obtained by this procedure was then transformed back to the corresponding cover value.

The classification was performed with the TABORD computer programme (van der Maarel et al. 1978; see also Persson 1977) using an initial manual classification comprising 10 groups. The programme was instructed to form 6 terminal groups (corresponding to a fusion limit ~ 0.75), and the minimum number of stands allowed in a group was set to one on account of the low total number of stands. The number of terminal groups was determined from several previous treatments by TABORD, where different parameters were used. Groups that were easily characterized in the table and corresponded to types, also recognizable in the field were considered as valid terminal groups. No threshold value was used on account of the homogeneity of the vegetation. The similarity coefficient used was the SIMILARITY RATIO by Westhoff and van der Maarel (1973).

An ordination of the stands was made in order to find succession trends, but also as a complément to the classification. The computer programme used was ORDINA (Roskam 1971; see also Persson 1978) which has a normalized Euclidean distance $ED/\sqrt{N}$ as a dissimilarity index.

Both the classification and the ordination were based on untransformed cover values and included only the bottom layer species.

The nomenclature for vascular plants follows Lid (1974), for bryophytes Nyholm (1954) and Arnell (1956), and for lichens Gams (1967) and Dahl & Krog (1973).

4 RESULTS

4.1 Classification

The communities are named by their dominants except for the Cladonia glauca - C. mitis community where the latter species is added as a suffix in order to avoid confusion with the Cladonia glauca - C. chlorophaea community on the outer dunes (Magnusson 1981).

The Cornicularia aculeata community usually colonizes large exposed sand areas with small amounts of accumulated litter, especially in oak areas. Cornicularia aculeata is usually the pioneer cryptogam but can be preceded by crusts of algae (sometimes lichinized). More commonly Cornicularia is associated with Corynephorus canescens and is often in exposed sites, the only cryptogam occupying the space between the grass tufts. Cladonia coccifera and C. mitis are two characteristic and early colonizers in the community.

The Cladonia glauca - C. mitis community has a much smaller distribution than the corresponding community on the outer dunes as a result of a small amount of litter. Where Corynephorus canescens and Carex arenaria have produced a debris layer that remains on the ground the Cladonia glauca - C. mitis community are able to colonize. Stand 18 (Table 1) represents a site where a vigorous Corynephorus canescens vegetation, possibly resulting from favourable moisture conditions, on the north side of a group of trees, has given rise to a litter layer. The good moisture conditions are indicated also by the appearance of mosses (Pohlia nutans and Dicranum scoparium). The lichen vegetation in stand 7 represents a common type in the limit zone between the inner and outer dune systems where Corynephorus canescens, Carex arenaria and Ammophila arenaria contribute with litter. The most conspicuous litter accumulation is that produced by pine needles on sheltered places where a continuous humus layer

covers the ground. In such sites (Stand 11) the community resembles a type of the Cladonia glauca - C. chlorophaea community found on a south-exposed dune ridge on the outer dunes. In both cases Cephaloziella divaricata forms cushions overgrown by Cladonia glauca and C. coccifera, and in the community from the outer dunes also by Cladonia cornuta and C. chlorophaea.

Lichen mats dominated by Cladonia zopfii are uncommon although the species is rather frequent, occurring as a colonizer in blowouts, or more often in somewhat protected sites often together with C. uncialis. Cladonia zopfii colonizes in blowouts on the northeastern slope while Cornicularia aculeata colonizes on the southwestern slope.

The Cladonia mitis community is common in protected sites such as on gentle slopes, on open sand patches in dwarf shrub heath and in pinewood. Although Cladina species dominate (besides C. mitis also C. impexa) other cryptogams are also common on account of the Cladina mats seldom being completely continuous but allow smaller bryophytes and lichens to exist in gaps. The mode of growth of Cladonia gracilis, with its proliferating cups, allows it to avoid overgrowing by the Cladina species and to become locally dominant. The species is not bound to Cladina mats but has a wide distribution, occurring also as a colonist on humus-covered as well as on humus-poor ground.

The Cladonia impexa community, found in one very sheltered site on a sand patch in dwarf shrub heath (Stand 8) is similar to the Cladonia impexa community on the outer dunes (Magnusson 1981). Cladonia rangiferina is however only rarely encountered in the Ammophila vegetation on the outer dunes and Cladonia tenuis, which is a common member of the community in Calluna-Empetrum heath on the outer dunes has not been observed outside this habitat.

The common Cladonia uncialis - C. mitis community colonizes smaller and more protected patches of sand with some litter accumulation than the Cornicularia aculeata community and is common especially in pine woods. In more open sand areas the community is usually associated with Corynephorus canescens whereas in pine woods sheltered conditions and a stabilized sand surface may be formed through the closure of the surrounding vegetation. Cladonia uncialis is the pioneer while Cladonia mitis reaches codominance at a later stage. In well-developed mats few other species are of importance due to the ability of Cladonia uncialis to nearly completely fill up the gaps between the Cladina cushions. The two dominants are either in balance or Cladonia mitis has a competitive advantage through bending the podetia over C. uncialis.

4.2 Ordination

The extracted variance for the first five dimensions in the ORDINA-ordination was 20, 18, 15, 13 and 8% respectively or together 74%. The variance presented in each of the diagrams in Figures 1-3 including the first four dimensions is therefore about the same. The results of the ordination and classification agree fairly well as each TABORD group is recognizable in at least one of the ordination diagrams. One of the groups, that comprising Stand 8, is sharply delimited in all diagrams. The similar extracted variance for the first dimensions implies a spherical hypervolume with no pronounced species gradients. The vegetation material has a large contribution of species with low cover common to all stands and a few dominating species (Cornicularia aculeata, Cladonia glauca, C. mitis, C. impexa, C. uncialis and C. zopfii) which separate the stands in different directions.

If the lichens are divided into volume lichens and surface lichens (Magnusson 1981) the stands may be arranged along axis 1 according to a combined species gradient. Included in the surface lichens

are foremost the small Cladonia-species such as C. glauca, C. coccifera, C. cornuta, C. chlorophaea, C. floerkeana, C. subulata, C. scabriuscula, C. pityrea, C. fimbriata and C. squamosa but also Cornicularia aculeata and the two Lecidea-species. Included in the volume lichens are the Cladina-species, Cladonia zopfii, C. uncialis, C. gracilis, Cetraria islandica and Cornicularia muricata. These species do not suffer from overgrowing and are themselves often able to overgrow other lichens on account of growth form (large volume, often cushion growth form and upright growth). The limit between the two groups is of course not very sharp. In Figure 3 isolines for the quotients between the added contributions of volume lichens and surface lichens after transforming the cover values to 1/32nds (1, 3, 6, 12 and 24 respectively) are given. An increasing proportion of volume lichens both within and between the TABORD groups to the right along the first axis is interpreted so that a development of a certain stand to the right along this axis within certain limits is likely. The continuous carpets formed by Cladonia mitis in association with C. uncialis give high values of the quotient between volume lichens and surface lichens, especially in sheltered sites where the mats are thick. The more heterogenous mats with Cladonia mitis and C. impexa also enable surface lichens to exist and thus high quotients are exceptional, as for instance in Stand 8. In this site a dense and thick Cladonia impexa carpet has been produced.

5 DISCUSSION

The prerequisite for the lichen colonisation is a stable or nearly stable sand surface (Fig. 4). Sand is not a necessary substrate, except for Cladonia zopfii, which in the Sand-hammaren area is only found on sand. The other species are found both in Calluna-Empetrum heath and in pine woods. The stabilized sand surface may serve as an obstacle and anchorage for thallus fragments. For instance, Cornicularia aculeata is considered a rapid colonizer by means of windborne thallus fragments (e.g. Warming 1909), which blow over the sand and come to rest around obstacles (Stewart & Patton 1924).

A rapid colonization in addition to the ability to withstand exposed conditions explains the abundance of Cornicularia aculeata on newly stabilized sand patches. A succession towards a Cladina-dominated lichen vegetation is however to be expected in due course as a consequence of a later establishment and increasing protection through the successively closing surrounding vegetation. The vascular plants therefore influence the cryptogamic vegetation in an indirect way. Such a development is indicated by the intermediate Stand 6 which links the Cornicularia aculeata and Cladonia mitis communities (Table 1, Figure 3). Although no Cladina mats have been observed which apparently have been pioneer vegetation, a Cornicularia stage is probably not necessary for the preparation of the ground. The contribution of Cornicularia aculeata to sand fixation is probably small.

On the outer dunes it was found that the Cladina species (Cladonia impexa) had low abundance despite suitable localities whereas the Cladonia glauca-dominated lichen vegetation luxuriated, an observation that was ascribed to differences in rate of spread (Magnusson 1981). The same relation ought to prevail in protected sites on the inner dunes where litter has accumulated. A succession to a Cladina-dominated and at the same time Cladonia uncialis-dominated stage is

suggested by Stand 7 (Table 1, Figure 3). Cladonia impexa may possibly become more favoured than C. mitis in these sites with soil conditions resembling those on the outer dunes.

For establishment on the extremely exposed northeastern slopes of blowouts with rather mobile sand a rapid colonization is of secondary importance in comparison to the ability to withstand the environmental conditions. Cladonia zopfii has this ability when it occupies this habitat usually as the only cryptogam. The species sustains some removal of sand and survives on account of a well-developed system of rhizines (Böcher 1952). Whether the position of Stand 4 along axis 1 (Fig. 3) also implies a succession towards a Cladina- and Cladonia uncialis-dominated stage is uncertain. Böcher (1941b) regards a Cladonia mitis-dominated lichen vegetation to be a final stage that arises simultaneously with the closing of the surrounding vegetation. The presence of the species also in Cladina mats (Stand 10 and 16) in addition to an upright growth (volume species) indicates however that the species can persist over longer periods.

For a large occurrence of Cladonia uncialis in the moderately exposed sites the species usually occupies a rapid colonization is a necessity as such sites are potential habitats for the Cladina species. Krieger (1937) characterizes the species as one of the earliest colonizers on humus-covered ground. Later it becomes superseded by the Cladina-species (Cladonia sylvatica and C. rangiferina). The observation that Cladonia mitis sometimes bends the podetia over Cladonia uncialis indicates that a succession towards Cladina-dominated lichen mats is possible also at Sandhammaren. As a rule however Cladonia uncialis at Sandhammaren ought to be regarded to be a member of a lichen final stage (Fig. 4).

6 CONCLUSIONS

The pioneer cryptogamic vegetation on both dune systems is strongly dominated by lichens as the result of an open dry habitat with a sparse phanerogamic vegetation and lack of competition from mosses. On the outer dunes the rapid invasion by the Calluna-Empetrum heath together with the simultaneous expansion of mosses results in the life time of the pioneer lichen vegetation only being long enough in exposed sites to allow successions among the lichens themselves. The colonization over a homogeneous litter substrate ensures a uniform lichen vegetation. The slow invasion of the dwarf shrubs on the inner dunes means that there is time for the effects of competition to lead to differentiation in the lichen mats so that succession favours large species. Variations in amount of litter and degree of exposure further differentiate the composition of the lichen mats. The result is a slightly higher species number among the pioneer lichen vegetation on the inner dunes than on the outer dunes and the dominance of one or more species in the different sites.

7 SUMMARY

The cryptogamic vegetation, dominated by lichens, in a secondary coastal dune area is described. The Cornicularia aculeata community colonizes large exposed sand patches. The Cladonia glauca - C. mitis community colonizes where litter has accumulated. The Cladonia mitis and C. impexa communities occupy more sheltered sites than the Cornicularia aculeata community. The scattered Cladonia zopfii community colonizes both exposed and slightly more sheltered sand patches. The common Cladonia uncialis - C. mitis community usually colonizes smaller sand patches with some humus accumulation than those colonized by the Cornicularia aculeata community. The Cladonia mitis, the C. impexa and the Cladonia uncialis - C. mitis communities and probably the Cladonia zopfii community are suggested to be final stages in the lichen succession.

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Table 1. The lichen communities with frequency and mean degree of cover (the exponent) for the different species

Stand no.	Cornicularia aculeata- community				Cladonia glauca- C. mitis-community				Cladonia mitis-community				C. impexa- community	Cladonia zopfii community	Cladonia uncialis- C. mitis-community						
	6	9	15	17	7	11	18	1	3	5	10	12			14	16	8	4	13	1	2
Cornicularia aculeata	100 ⁴	100 ⁴	100 ⁴	100 ³	100 ²	86	50	100	90	100	92	64	100	20	21	65	93	100 ²	95	21	
Cladonia glauca	100	80	100	100	100 ³	100 ⁴	100 ²	100	100	100	91	100 ²	71	94	100	5	90	100 ²	100	5	
" coccifera	95	100	100	100 ²	100	100 ³	100	90	100	100	100	7	75	80		65	93	50	75	7	
Cephalozelia divaricata	79	90	36	86	42	100 ³	85	81	100	91	96	14	100 ²	10	21	80	100		90		
Cladonia gracilis	16	17	21		100 ²	29	55	95	100 ³	100 ³	8	43	75	100 ⁴	21	100 ²	79	100	5	29	
" impexa	21	10	43		100 ²	52	10	90 ²	100 ²	75 ²	4	79 ³	44	20	100 ⁵	70	7	79	15	71	
" mitis	100 ³	83	57	64	100	67	70	100 ⁴	100 ³	100 ²	100 ⁴	100 ³	100 ³		74	95 ²	100	100 ³	95 ²	100 ³	
" zopfii						10					88					100 ³	100 ³	64 ²			
" uncialis	42	7	7	14	100 ³	62	65	57	80	66		57	100		26	100 ³	29	100 ⁴	100 ⁴	100 ⁴	
" chlorophaea	47	67	79	79	79	86	80	90	50	50	60	71	25	90		35	79	64			
" floerkeana	21	30	100	86	37	48	20	62	20	16	16	7		30		10	7	7			
" cornuta	32	17	29		26	19	20	29	40	8	8	7	13	10	21			21			
" subulata	5	53	93	86		76	100	5	25	36	14	31	50		5	15			10		
" pityrea	7	36	79		16	71	85	71	10		40	29	6	60		5	14				
Dicranum scoparium				21	5	19	55	5	25	80 ²	7			10		50			14		
Lecidea granulosa	20	86	36		24	45		5	10		7	31				10	36				
" uliginosa	3	7			14	20			8	8		6				5	21	5			
Cladonia arbuscula								14	90	25	57				26	20		15	79 ²		
Hypogymnia physodes	5	3	14			25									5	10		29			
Pohlia nutans					5	95 ²		10			10				5	35			5		
Cladonia rangiferina					5	5		10							100 ²						
Ceratodon purpureus	3														16				5		
Polytrichum piliferum						5									5			25			
Cladonia scabriuscula						10			16						5						
Cornicularia muricata					60						8				5						
Cladonia fimbriata																					
Cetraria islandica											7			10							7
Cladonia squamosa												38									
Polytrichum juniperinum															5						
Ammophila arenaria								5	10												
Carex arenaria	58	17			79	25									95	5	64		15	71	
Corynephorus canescens	79	87 ²	21	43	42	24	100	71	50	88	36	19	70		11		21	29	45	36	
Deschampsia flexuosa											4		20								
Festuca polesica																		14			
Pinus sylvestris juv.											4		10							29	
Salix arenaria																		36			
Viola canina																		7			
Vegetation cover %	59	51	56	61	77	69	72	75	62	75	72	75	58	80	77	72	72	73	66	72	
Number of samples	19	30	14	14	19	21	20	21	10	12	25	14	16	10	19	20	14	14	20	14	
Size of the stand m ²	5.1	13.0	4.5	6.0	6.0	22.8	13.8	8.8	2.5	3.8	11.3	16.9	10.1	3.8	6.6	6.3	11.3	5.6	20.0	1.0	

Table 1 continued:

Notes on location, exposure and whether any considerable litter accumulation occurs, for the different stands are given below. The position of a stand is defined as sheltered when the stand is sheltered in such a way that microclimatological extremes are reduced either through its position on a north slope or through surrounding vegetation.

- Stand 1: Sheltered position on a gentle north slope to to the east of a group of pines.
- " 2: Sheltered position on a sand patch in a *Calluna-Empetrum* heath.
- " 3: As stand 2.
- " 4: Sheltered position on a gentle east slope in a *Pinus mugo* plantation surrounded by trees in all directions.
- " 5: Rather exposed position on a gentle west slope, west of a small oak, otherwise surrounded by sand patches.
- " 6: Exposed position in a small blowout with no shelter in an open sand area.
- " 7: Sheltered position on a sand patch in a *Calluna-Empetrum* heath. *Carex arenaria* and *Corynephorus canescens* have given rise to a litter layer.
- " 8: Extremely sheltered position by a *Calluna-Empetrum* heath in three directions and a low dune ridge in the fourth direction.
- " 9: Exposed position in a small blowout in an open sand area. The sand surface is influenced by digging activities of ants.
- " 10: Sheltered position along the northern edge of a group of pines. The ground surface contains litter from *Corynephorus canescens*.
- " 11: Sheltered position along the western edge of a blowout, to the east of a pine wood. Pine needles form a litter layer.
- " 12: Sheltered position in an opening in a pine wood.
- " 13: Exposed position on a gentle south slope in an open sand area in a pine wood. Pine needles are common on the ground.
- " 14: Sheltered position on the lower part of the eastern slope in a blowout to the east of a group of pines.

- Stand 15: Sheltered position in an open sand area in a pine wood, bordering on Calluna-shrubs in its western part.
- " 16: Sheltered position in an opening in a pine wood with accumulation of pine needles.
- " 17: Exposed position on a gentle east slope in an area with open sand to the east of a group of pines, some accumulation of pine needles.
- " 18: Sheltered position along the northern edge of a group of pines. Litter from *Corynephorus canescens* and pine needles on the ground.
- " 19: Sheltered position on a gentle south slope in an opening in a wood of pines and oaks.
- " 20: Sheltered position in an opening in a pine wood.

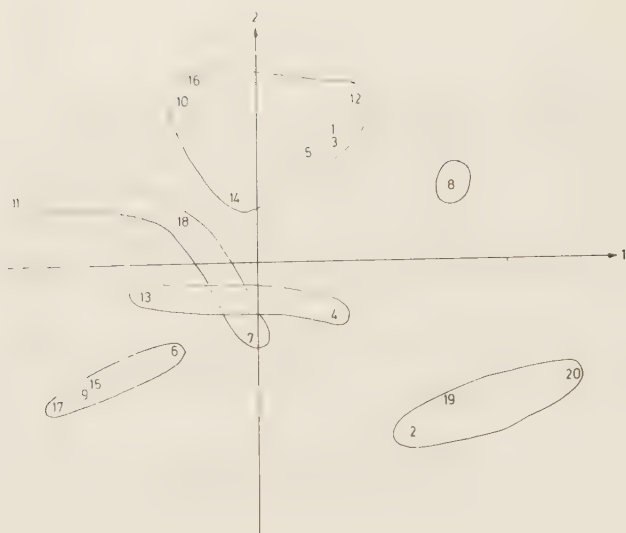


Fig. 1. Standordination (dimension 1,2) with the TABORD groups indicated.

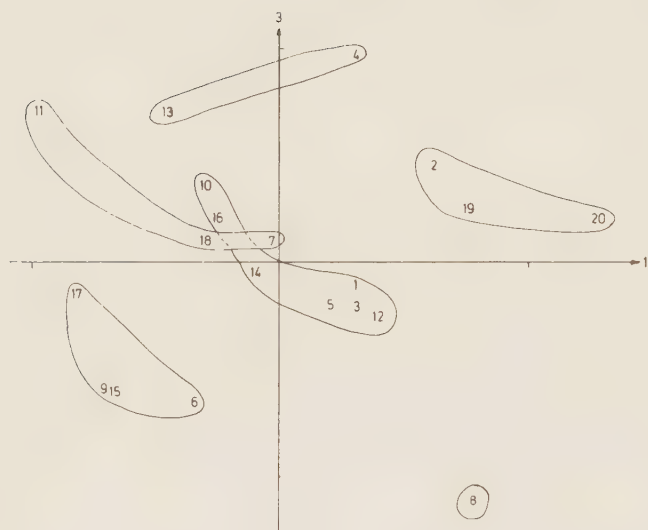


Fig. 2. Standordination (dimension 1,3) with the TABORD groups indicated.

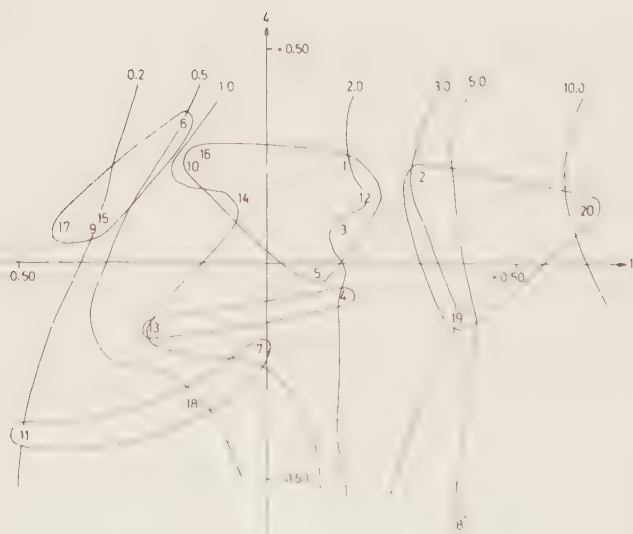
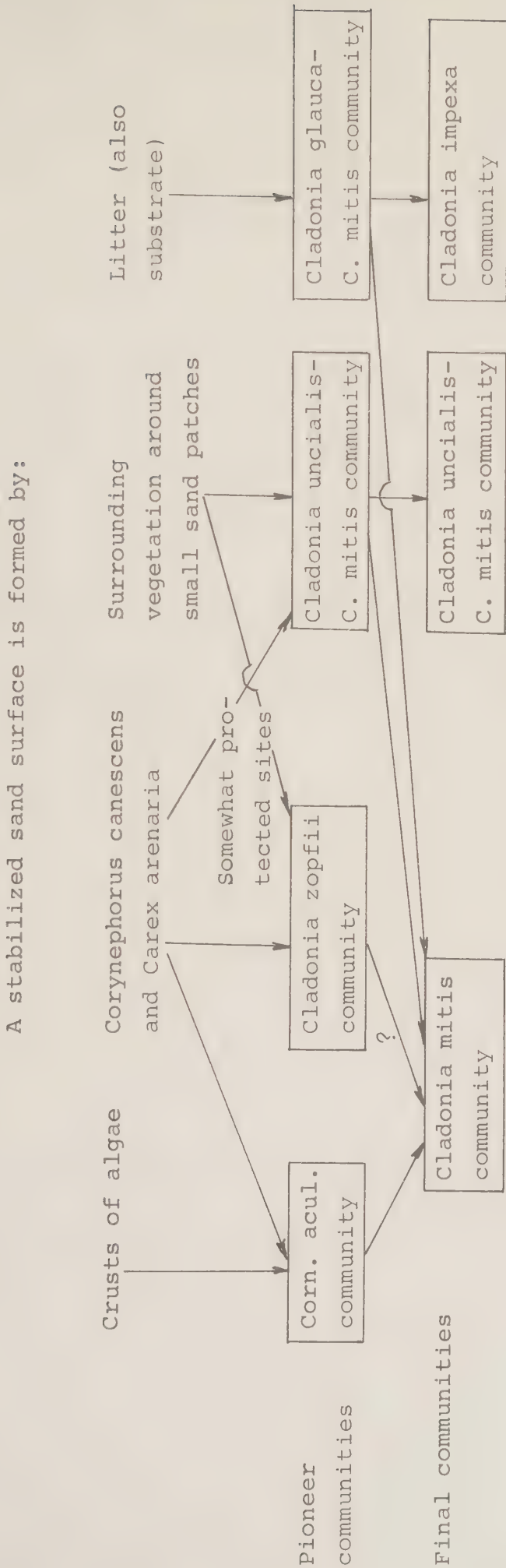


Fig. 3. Standordination (dimension 1,4) with the TABORD groups and isolines for the quotient between cover of volume lichens and that of surface lichens indicated.

Fig. 4. Suggested succession scheme for the bottom layer



FREQUENCY DETERMINATIONS WITH DIFFERENT QUADRAT SIZES IN
TWO PLOTS ABUNDANT IN LICHENS IN A COASTAL DUNE AREA IN
SOUTHERN SWEDEN

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1 INTRODUCTION

For describing and analysing vegetation, the frequency method, that is the determination of the number of samples in which a species is present relative to the total number analysed, is both objective and rapid. The advantages are, however, counteracted by the fact that it is difficult to know what is really being measured as the achieved frequency value depends on the quadrat size as well as on the distribution, the density (the number of individuals per unit area) and often the size of the individuals (Goodall 1952). As these characters vary from species to species, the frequency becomes a poor measure of the abundance. Raunkiaer was not aware of the weakness of the frequency value as a quantitative measure in his first paper from 1909, but later (1913) he wrote that in doubtful cases a combination of frequency values and subjective estimations of the relative amount of a species according to a scale (e.g. 1-5) must be employed. DuRietz (1921) criticized Raunkiaer's ideas, after testing the frequency method using different quadrat sizes. He found a poor agreement between cover and frequency and considered the sample size (0.1 m^2) recommended by Raunkiaer was too large as it allowed several species to have 100% frequencies.

Goodall (1952) treated the relation between sample size and frequency of a species and said that the inadequacy in quantity can only be overcome by diminishing the quadrat size to infinity - the point - in which case the distribution ceases to have an effect. Daubenmire (1968) discussed the case when more than one species has 100% frequency and wrote that this could only be allowed when the sample size would otherwise be so small that many rare species would be missed. A split into a large number of quadrat sizes is, however, not desirable for the sake of comparison of different investigations and

that is why standard sizes have been suggested. Cain and de Castro (1959) suggested a quadrat size of 0.01 or 0.1 m² for the bottom layer as optimal.

In this investigation the frequency method is tested in two plots abundant in lichens, representing different types of cryptogamic colonisation in a coastal dune area at Sandhammaren in southern Sweden. One of the plots is from the outer grey dunes with a litter covered ground and the other from the inner dunes with an eroded sand surface with a sparse litter layer. The plots were analysed bearing the following questions in mind: How good is the frequency as a quantitative measure of the cover of the different species? Which quadrat size should be chosen for different purposes in the frequency analyses? How are the results related to the different ways of colonization in the two dune systems represented by the plots?

2 THE INVESTIGATION AREA

The dune area at Sandhammaren (14°11'E and 55°22'N) is situated in SE Skåne, southernmost Sweden. The general outlines and succession of the vegetation in this dune area has been treated by Olsson et al. (1971) and Olsson (1974) and the bottom layer has been described by Magnusson (1981a and b). The outer dunes of primary origin are often arranged in ridges of different ages and are covered by vegetation. The inner irregular dunes of secondary origin are often bare and blowouts are common.

On the outer dunes the sand is being stabilized by the dune grasses Ammophila arenaria and A. baltica and to a lesser degree by Elymus arenarius. In its inner part the dune grass zone is being replaced by a dwarf shrub heath (Calluna vulgaris and Empetrum nigrum) which in turn is being invaded by trees (birch, pine and oak). Bryophytes and lichens colonize simultaneously. The lichens dominate on the outer dunes and are represented mainly by small Cladonia species (Cladonia glauca, C. chlorophaea, C. cornuta etc.). Where dune ridges

are developed the Ammophila-vegetation persists on south slopes even in the dune heath. The bottom layer is about the same as on the outer dunes but gradually becomes overgrown by Cladonia impexa. On the northern slope of the ridge with still scattered dwarf shrubs Dicranum scoparium and to a lesser degree Cladonia impexa form mats. The bottom layer in the closed heath may be poorly developed or consists of moss patches dominated by Pleurozium schreberi or Cladina mats dominated by Cladonia impexa. The final vegetational stage in present day succession in the area is either oak wood or pine wood of which the latter sometimes is light enough to allow a well developed cryptogamic layer with carpets of Pleurozium schreberi and Cladina species.

The human influence on the inner dunes was previously great due to the grazing and devastation of trees and bushes. In this area Corynephorus canescens and to a lesser degree Carex arenaria, as well as lichens stabilize the sand surface. The succession continues via a Calluna vulgaris dominated dwarf shrub heath to either oak wood or pine wood. Pine seedlings can already also colonize the lichen mats. Common constituents of the lichen mats are: Cornicularia aculeata, Cladonia mitis, C. impexa, C. coccifera, C. glauca, C. gracilis, C. uncialis and more scattered C. zopfii. Where the lichen mats are concerned there are also changes in species composition according to age. For instance, a Cladonia impexa and C. mitis dominated lichen vegetation is suggested to follow after a Cornicularia aculeata-stage in sheltered sites.

3 MATERIAL, METHODS AND NOMENCLATURE

Two homogeneous plots were selected from the two dune systems in lichen dominated vegetation types. Plot 1 is from the outer dunes on the south slope of a ridge parallel to the sea (the fourth from the sea according to Magnusson 1981a) 1.2 km SSW of the lighthouse at Sandhammaren. The vascular plants (mainly Ammophila arenaria and A. baltica, Carex arenaria and Corynephorus canescens) have produced a well developed litter layer which is colonized by subulate and scyphous Cladonia-species (Cladonia glauca - C. chlorophaea community, Magnusson 1981a). The bottom layer covers about 50% of the ground. Plot 2 is from the inner dune landscape on a gentle north-facing slope 0.6 km SW of the lighthouse. Scattered Corynephorus canescens, Carex arenaria and Ammophila arenaria have given rise to only a fragmentary litter layer. The lichens are dominated by Cladonia mitis and C. impexa. In this case the bottom layer covers about 80% of the ground.

'Shoot frequency' (Greig-Smith 1964) was determined in overlapping quadrats of six different sizes (1.6X1.6, 3.1X3.1, 6.3X6.3, 12.5X12.5, 25X25 and 50X50 cm respectively). The quadrats were demarcated by a wooden frame representing the largest quadrat size and by nylon-threads with the smallest quadrat size in the middle. The species found in the smallest quadrat were therefore common to all quadrats. The investigated plots, 11 m² in Plot 1 and 7.5 m² in Plot 2, were entirely taken up by sample units of the largest quadrat and consequently a total of 44 and 30 units were analysed in Plot 1 and Plot 2, respectively. The evaluation of the frequency as a quantitative measure was made as a comparison to the order of the species ranked in accordance to frequency in quadrats of different sizes, and the order of the species ranked according to the cover over all the plots. The ranking according to cover could be established only for the most common species, in Plot 1 for 9 species and in Plot 2 for 10 species. The remaining species were about equally uncommon and were hardly separable. The analyses were carried out in July and August 1977.

The nomenclature for vascular plants follows Lid (1974) except for the hybrid between Ammophila arenaria and Calamagrostis epigeios, which is called Ammophila ballica in this case. The nomenclature for bryophytes follows Arnell (1956) and Nyholm (1954-69) and for lichens Dahl & Krog (1973) and Gams (1967). Cephaloziella divaricata may include other Cephaloziella species and Cladonia floerkeana may include C. bacillaris as well.

4 RESULTS

The agreement between the order of the species based on frequency and cover is rather good in Plot 1 (Tab. 1, Fig. 1). Cladonia glauca is a dominant or codominant in all the quadrats. A poor agreement is, however, shown by Cladonia impexa, that is considerably lower ranked in the frequency order than in that based on cover. In Plot 2 the agreement between cover and frequency is poor (Fig. 2, Tab. 2). Cladonia mitis and C. impexa are codominants according to cover and do not achieve the same frequency (100%) until in the largest quadrat. The two less common species, judging by cover, Cladonia glauca and C. coccifera, have a high rank in the frequency list in most quadrat sizes. The opposite is valid for Cladonia zopfii, third in the cover order. In the frequency list this species is only in ninth place in the largest quadrat size.

The range of the average frequencies for the bottom layer species is fairly similar in Plots 1 and 2 - from about 15 to 60 and 66% respectively (Tables 1 and 2).

If one sample was taken from the smallest quadrat size this would contain an average of about 2 species (Tables 1 and 2). If one sample was taken from the largest quadrat size this would contain an average of 9 species in Plot 1 and 12 in Plot 2. The total number of bottom layer species in Plot 1

is 14 and 20 in Plot 2. If 44 and 30 samples were taken from these two plots with the smallest quadrat size 5 and 6 species respectively would be lacking while all the species were present in the samples from the 25 x 25 cm quadrat.

In Plot 1 no concentration of species on any part of the plot can be seen in the primary Tables. In Plot 2 four species, Pohlia nutans, Cephaloziella divaricata, Cladonia zopfii and C. pityrea are mainly concentrated on that half of the plot that forms the upper part of the slope. The distribution of Pohlia nutans probably indicates a moisture gradient. Cladonia uncialis has a distribution concentrated on three parts of the plot.

5 DISCUSSION

If the main reason for the frequency analyses is a qualitative description then the stress is laid upon obtaining as complete a floristic composition as possible. This can be achieved by making a few samples from a large quadrat or by taking many from a small one. The optimal quadrat size becomes a compromise between too large a one with about the same species composition in all samples and too small a one with a large variation of samples but with some species missing or poorly represented. In the two examples related here the two largest quadrat sizes are regarded as being too large in both plots on account of the presence of several species in all or nearly all of the samples. If all the species found in the plots are to be included the next largest quadrat size must have to be used unless the number of samples of a smaller size are not to be increased considerably. However, in Plot 1 only one species, Hypogymnia physodes of the least frequent species is regarded as characteristic for the described lichen vegetation (cf Magnusson 1981a) and therefore ought to be sampled. This was accomplished by the quadrat of the size 6.3 x 6.3 cm. In Plot 2 no individual less frequent species is regarded as

more characteristic than another (cf Magnusson 1981b) why the 6.3 x 6.3 cm quadrat size is subjectively regarded as a minimum where three of the six least frequent species are present. The optimal quadrat size in both plots concerning qualitative description is therefore considered to be either 6.3 x 6.3 cm or 12.5 x 12.5 cm.

As the frequency is usually a less useful measure of the abundance frequency analyses are less suitable for estimating quantitative relations between species. The rather good agreement between cover and frequency in Plot 1 is probably an exceptional case. However, the frequency method offers good possibilities for comparing the appearance of one species or a defined group of species along spatial or temporal gradients. An average frequency value is calculated for a group of species. The method detects changes most sensibly if the frequency value is around 50% at the start of the gradient. If all species in the plots are included in a group then the quadrat size becomes 12.5 x 12.5 cm or 25 x 25 cm in plot 1 and 25 x 25 cm in plot 2.

For combined qualitative and quantitative frequency analyses in Plot 1 the optimal quadrat size becomes 12.5 x 12.5 cm, in Plot 2 12.5 x 12.5 cm or 25 x 25 cm and in both plots 12.5 x 12.5 cm. This quadrat size agrees largely with Daubenmire's (1968) recommendation that a quadrat size should be large enough to allow one species to reach 100% frequency in order to obtain as large a range of frequency values as possible.

There are two indications, apart from the information regarding distributions from the primary tables, that the species in Plot 1 are more evenly spread out over the plot surface than the species in Plot 2. The probability of finding any one species within a certain quadrat size, that is the average frequency, is about the same in both plots, despite higher total cover of the bottom layer in Plot 2. There are also fewer curves with "knees" in Plot 1 than in

Plot 2. The "knees" indicate a considerably increased probability of finding a species within one quadrat size than in the previous smaller one. This in turn indicates a distribution in patches, which are considerably more often sampled by one quadrat size than the previous smaller one.

A patchy distribution can be the result of colonization, competition or way of growth. The humus colonizer Cladonia glauca (Krieger 1937, Magnusson 1981a) has a much more irregular curve shape in Plot 2 than in Plot 1. The dead remains of Corynephorus canescens and Carex arenaria in Plot 2 ought to have frequency "knees" like the living plants (Table 2) and thereby also cause "knees" for Cladonia glauca. Irregular curves may also probably be the result of mere chance where the propagules land and sometimes enhanced by the sampling methodology. In Plot 1 the dominating species propagate by means of thallus fragments (Klement 1955) or ascospores and conidia, which require an association with an alga (Ahti 1961) and this is the reason why a more accidental colonisation is probable. A remarkable exception is made by Cladonia mitis with regular curves in both plots. Overgrowing from the Cladina-species may have caused or contributed to the irregular curves of the first two of the three uncompetitive species Cornicularia aculeata, Cladonia glauca and C. coccifera (Surface lichens, Magnusson 1981a). A cushion growth form like that of Cladonia impexa leaves gaps and a frequency rise can be expected when the quadrat size is large enough to cover the gaps.

The similar appearance of the lichens in Plot 1 with individual podetia of about equal size, evenly distributed, explains the agreement between the frequency and cover orders. The main exception that upsets the results is Cladonia impexa with hardly discernible individual podetia arranged in cushions. The different growth forms and distribution types represented in Plot 2 cause large deviations in the frequency and cover orders. The low frequency ranks of Cladonia uncialis and C. zopfii are easily explained by their

concentrated distributions. Cladonia glauca, C. chlorophaea and C. coccifera are so spread out over the plot, although with some irregularities suggested for the first species, that they achieve higher frequency values than several species with higher cover. Cladonia mitis is represented by a prostrate form with the podetia separated to a great extent. This way of growth gives the species a high frequency value also in the smallest quadrat. On the other hand the cushion growth of Cladonia impexa implies that the species gets low frequency values in relation to cover.

The investigation illustrates the two different kinds of cryptogamic colonisation in the two dune systems (Magnusson 1981a and b), both dominated by lichens. On the outer dunes r-selected species dominate. A fast and effective spread by these species is determined by the production of soredia. These lichen species colonize open humus covered patches in Ammophila-vegetation and Calluna-Empetrum heath. The individuals are small and they maximize the area of covered ground rather than maximizing the biomass produced in a given area. The lichens on the outer dunes have therefore a surface covering strategy. This ensures as large a number of offspring as possible in an unstable environment which is subject to overgrowing by e.g. Cladonia impexa, Calluna vulgaris and Empetrum nigrum and to being washed away by storm waves. On the other hand mortality caused by competition among the colonizers themselves is surely neglectable on account of the similar subulate or scyphous growth of about equal sized podetia.

The colonization of the inner dunes reveals conspicuous patches of lichens. In contrast to the relations on the outer dunes the substrate is not a necessary prerequisite, except for Cladonia zopfii, which is only found on sand. The other species have more optimal conditions in dwarf shrub heath or in pine wood. The environmental resource is a sheltered site where competition from the dwarf shrubs and the mosses is lacking for long time. Such sites originate slowly through a general overgrowing of higher plants of the sand

dunes. The scarcity of such sheltered sites and their long life span implies that the competition between the colonizing lichens is allowed time to differentiate the composition of the final lichen mat. Species with a volume occupying strategy will be favoured. On account of a large biomass they can overgrow and overshadow their neighbours. Cornicularia aculeata is a typical pioneer and r-species. Due to its depressed growth form it suffers from overgrowing from more upright growing species and in time becomes reduced in quantity. Other species that also occur as pioneers, above all Cladonia uncialis, C. zopfii and C. gracilis are r-species in this aspect but behave as k-species with relation to other species in the lichen mats. They have upright thalli and keep up with the most typical final species, Cladonia mitis and C. impexa, which are typical k-selected species. They usually invade at a later stage than the pioneers.

6 SUMMARY

Two plots, abundant in lichens, are analysed by means of overlapping quadrats of different sizes with respect to frequency. Plot 1 is from dunes near the sea where the dune grasses (Ammophila arenaria and A. baltica) stabilize the sand and give rise to a well developed litter layer. Plot 2 is from the inner dunes of secondary origin where Corynephorus canescens and Carex arenaria are scattered and the litter cover is sparse. In Plot 1 the cryptogamic species (e.g. Cladonia glauca, C. cornuta, C. coccifera, C. impexa and Cephaloziella divaricata) to a great extent have single podetia evenly spread out, while in Plot 2 the species (e.g. Cladonia mitis, C. impexa, C. zopfii and Cornicularia aculeata) represent different growth forms and distribution types. This explains why a fairly good agreement is found in Plot 1 between orders of the species based on cover and frequency respectively while in Plot 2 a poor agreement is found. Of the investigated quadrat sizes the size 12.5 x 12.5 cm is suggested as optimal for frequency analyses in the both plots.

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Table 1.

Frequency (%) in plot 1. Number of samples = 44. Rank order of the species in the bottom layer according to frequency in brackets.

Species	Size of quadrat in cm ²	2.4	9.7	39	156	625	2500	Rank order according to cover
<i>Cladonia glauca</i>		45(1)	73(1)	98(1)	98(2)	100(1)	100(1)	1
<i>Cephaloziella divaricata</i>		27(2)	55(2)	89(2)	100(1)	100(1)	100(1)	5
<i>Cladonia coccifera</i>		23(3)	52(3)	75(3)	89(3)	100(1)	100(1)	3
<i>Cladonia cornuta</i>		18(4)	43(4)	66(4)	84(4)	98(4)	100(1)	2
<i>Cornicularia aculeata</i>		14(5)	18(5)	50(5)	61(6)	73(6)	98(6)	6
<i>Cladonia chlorophaea</i>		9(6)	18(5)	34(6)	64(5)	91(5)	100(1)	7
<i>Cladonia floerkeana</i>		5(8)	9(7)	11(8)	27(7)	64(7)	89(7)	8
<i>Cladonia impexa</i>		9(6)	9(7)	16(7)	25(8)	57(8)	86(8)	4
<i>Hypogymnia physodes</i>		-	-	2(11)	14(9)	23(9)	52(9)	.
<i>Lecidea uliginosa</i>		-	5(10)	5(10)	9(11)	18(10)	43(10)	.
<i>Cladonia mitis</i>		2(9)	7(9)	9(9)	11(10)	14(11)	23(11)	9
<i>Dicranum scoparium</i>		-	-	-	-	2(14)	16(12)	.
<i>Cladonia subulata</i>		-	2(11)	2(11)	5(12)	7(12)	11(13)	.
<i>Cladonia pityrea</i>		-	-	-	2(13)	5(13)	9(14)	.
<i>Cladonia indet.</i>		32	41	41	41	43	43	.
<i>Carex arenaria</i>		39	70	84	98	100	100	.
<i>Ammophila baltica</i>		5	7	9	9	20	32	.
<i>Ammophila arenaria</i>		7	7	9	11	18	27	.
<i>Corynephorus canescens</i>		-	-	-	2	9	18	.
<i>Koeleria glauca</i>		-	-	-	-	2	2	.
Average frequency for the bottom layer (<i>Cladonia</i> <i>indet.</i> excluded)		17	26	38	45	54	66	
Average number of spe- cies per sample (<i>Cladonia</i> <i>indet.</i> excluded)		1.5	2.9	4.7	6.0	7.7	9.4	

Table 2.

Frequency (%) in plot 2. Number of samples = 30. Rank order of the species in the bottom layer according to frequency in brackets.

Species	Size of quadrat in cm ²						Rank order according to cover
	2.4	9.7	39	156	625	2500	
<i>Cladonia mitis</i>	57(1)	83(1)	93(1)	97(1)	100(1)	100(1)	1
<i>Cladonia glauca</i>	20(4)	43(2)	50(2)	83(2)	97(3)	100(1)	10
<i>Cladonia chlorophaea</i>	7(9)	30(5)	50(2)	80(3)	100(1)	100(1)	.
<i>Cladonia gracilis</i>	10(7)	27(7)	47(4)	73(4)	97(3)	100(1)	4
<i>Cladonia coccifera</i>	13(6)	30(5)	40(8)	63(6)	80(6)	100(1)	9
<i>Cladonia impexa</i>	23(3)	27(7)	43(6)	53(7)	77(7)	100(1)	1
<i>Cornicularia aculeata</i>	20(4)	40(3)	47(4)	73(4)	90(5)	97(7)	5
<i>Cephaloziella divaricata</i>	-	7(11)	20(10)	33(9)	63(9)	80(8)	.
<i>Cladonia zopfii</i>	27(2)	33(4)	43(6)	50(8)	67(8)	77(9)	3
<i>Cladonia uncialis</i>	10(7)	17(9)	20(1)	30(10)	33(12)	67(10)	6
<i>Dicranum scoparium</i>	3(11)	7(11)	7(13)	17(13)	40(10)	60(11)	7
<i>Cladonia cornuta</i>	-	-	7(13)	13(15)	20(14)	53(12)	.
<i>Pohlia nutans</i>	3(11)	13(10)	23(9)	23(11)	40(10)	40(13)	.
<i>Cladonia pityrea</i>	3(11)	3(15)	20(1)	23(11)	27(13)	40(13)	.
<i>Cladonia floerkeana</i>	3(11)	7(11)	7(13)	17(13)	17(15)	33(15)	.
<i>Cladonia arbuscula</i>	7(9)	7(11)	7(13)	13(15)	13(16)	30(16)	8
<i>Lecidea granulosa</i>	-	-	-	-	7(17)	7(18)	.
<i>Cladonia rangiferina</i>	-	-	-	-	3(19)	10(17)	.
<i>Cladonia subulata</i>	-	3(15)	3(17)	3(17)	7(17)	7(18)	.
<i>Hypogymnia physodes</i>	-	-	-	-	3(19)	7(18)	.
<i>Cladonia indet.</i>	20	23	23	23	23	23	
<i>Corynephorus canescens</i>	-	3	7	13	30	60	
<i>Carex arenaria</i>	-	-	3	10	13	43	
<i>Ammophila arenaria</i>	-	3	3	3	3	3	
Average frequency for the bottom layer (<i>Cladonia</i> <i>indet.</i> excluded)	15	24	31	44	49	60	
Average number of spe- cies per sample (<i>Cladonia</i> <i>indet.</i> excluded)	2.2	3.9	5.4	7.6	10.0	12.3	

Figures 1 and 2 Frequencies as a function of area for the most common species.

